

FLORA COSTARICENSIS

Family #193 Scrophulariaceae

Family #193a Schlegeliaceae

Family #194 Bignoniaceae

Family #195 Pedaliaceae

Family #196 Martyniaceae

Family #197 Orobanchaceae

SCROPHULARIACEAE

By Kerry Barringer and William Burger

REFERENCES—W. D'Arcy, Scrophulariaceae, *in* R. Woodson et al., *Flora of Panama*. Ann. Missouri Bot. Gard. 66: 173–272. 1979. F. Pennell, The Scrophulariaceae of eastern temperate North America. Acad. Nat. Sci. Philadelphia Monogr. 1: 1–650. 1935. P. Standley & L. O. Williams, Scrophulariaceae, *in* *Flora of Guatemala*. Fieldiana, Bot. 24, 9(4): 319–416. 1973. D. Sutton, A Revision of the Tribe Antirrhineae, British Museum (Natural History) & Oxford Univ. Press, London, 576 pp. 1989. D. Sutton & R. Hampshire, Scrophulariaceae, *in* *Flora of Nicaragua* (unpublished manuscript). 1995. J. Thieret, The tribes and genera of Central American Scrophulariaceae. *Ceiba* 4: 164–184. 1954. J. Thieret, Supraspecific classification of Scrophulariaceae: A review. *Sida* 3: 87–106. 1967.

Herbs or subshrubs (rarely woody shrubs or trees), erect to decumbent or prostrate (rarely climbing), terrestrial to semiaquatic or aquatic, autotrophic or hemiparasitic, bisexual, stems without internal phloem, glabrous or with simple or branched, glandular or eglandular uni- or multicellular hairs; stipules absent. **Leaves** alternate, opposite, or verticillate, simple (rarely deeply pinnately lobed), distal leaves often reduced and intergrading with the floral bracts, leaf blades serrate to entire or deeply pinnately lobed, venation pinnate or less often palmate. **Inflorescences** racemes, spikes, thyrses, or panicles of cymes or of solitary (several) flowers in leaf axils, bracteoles present or absent on the pedicels, pedicels usually well developed. **Flowers** bisexual, small to large, often showy, calyx 4- or 5-lobed, or deeply divided to the base and sepals 4 or 5 (2), imbricate or valvate in bud, persisting

and often enlarging slightly in fruit; **corolla** united and tubular to campanulate, bilaterally symmetric and usually 2-lipped (rarely radially symmetric), lobes 4–5 (8), upper (adaxial) lip 2-lobed to emarginate, sometimes galeate, lower (abaxial) lip usually 3-lobed, tube saccate or spurred in some; **stamens** 2–4 (5), alternating with the lobes, usually of 2 unequal pairs, filaments borne on the tube, free, anthers with 2 (1) equal or unequal thecae, distinct or confluent, rarely awned, a staminode present or absent (rarely 2 or 3), a disc present or absent around the ovary; pistil solitary, ovary superior (or half inferior), 2-locular (rarely 1-locular near the apex or 3-locular), ovules usually many on 2 axile placentas, unitegmic, style 1, terminal, stigmas simple or 2-lobed. **Fruits** usually dry capsules (rarely baccate), dehiscence loculicidal or septicidal or both (rarely indehiscent), placenta often persisting; seeds usually many and small, usually with an ornamented testa or exotesta (sometimes smooth or winged), endosperm usually present, embryo small.

The family Scrophulariaceae includes 285 genera with between 4,000 and 5,000 species. The family is primarily north temperate, but with tropical montane species and cosmopolitan weeds. One of the largest genera, *Calceolaria* (300–400 spp.), is almost exclusively South American and montane. In this treatment we include 36 genera with 72 species, 18 of these being introduced or cultivated (see listing at end of family, p. 69). Costa Rica lies between two major areas of diversity for the family: one in Andean South America and one in Mexico and Guatemala. Among the southern elements are *Alonsoa*, *Calceolaria*, *Scoparia*, and *Stemodia*, while northern elements are *Castilleja*, *Hemichaena*, *Lamourouxia*, and *Russelia*.

Most Scrophulariaceae are recognized by their sympetalous tubular (usually two-lipped) corollas,

two-locular ovaries with many ovules on axile placentas, capsular fruits with many small seeds, and stems lacking internal phloem. Most species are herbs or small shrubs, and the corollas are often showy. There is great diversity in the form of corolla and pollination vectors (see C. M. Kampny, *Pollination and flower diversity in Scrophulariaceae*, Bot. Rev. 61: 35–366, 1995). Iridoid compounds are common in the family. The family includes many species cultivated as ornamentals and an important drug plant (*Digitalis*) but no important food, spice, or fiber plants. Interestingly,

a few of the most colorful genera (e.g., *Castilleja* and *Lamourouxia*) have not been utilized in ornamental horticulture because of difficulty in propagating their hemiparasitic species. Species likely to be mistakenly identified as Scrophulariaceae are found in Lamiaceae, Acanthaceae, and Gesneriaceae, as well as the other families included in this volume. Current molecular studies indicate that the Scrophulariaceae, as traditionally defined, are polyphyletic (Wagstaff & Olmstead, 1997). We retain the traditional circumscriptions of families in this series to facilitate information retrieval.

Key to Genera and Unusual Species of Scrophulariaceae

- 1a. Plants fully aquatic, only the inflorescences held above the water level; leaves submerged or floating, whorled, with pinnatisect filiform divisions [rarely collected] *Benjaminia reflexa*
- 1b. Plants aquatic, partly aquatic, or terrestrial, if aquatic the leaves floating or emergent and not with submerged filiform pinnatisect divisions 2
- 2a. Plants slender-stemmed twining or climbing, usually found in gardens and near habitations; leaves mostly alternate 3
- 2b. Plants erect or creeping on the ground or aquatic, not twining or climbing, found in a great many habitats; leaves alternate or opposite 5
 - 3a. Leaf blades reniform to orbicular, cordate at base, 10–35 mm long, alternate or rarely opposite; corollas 7–9 mm long, with a basal spur *Cymbalaria muralis*
 - 3a. Leaf blades often triangular-subcordate, to 60 mm long, always alternate; corollas 30–80 mm long, without a spur 4
 - 4a. Corollas 60–70 mm long; calyx 15–24 mm long; seeds with lateral wings around much of the seed *Lophospermum erubescens*
 - 4b. Corollas 30–40 mm long; calyx 9–15 mm long; seeds without thin wings *Maurandya*
- 5a. (from 2b) Leaves deeply dissected or compound, the lobes or leaflets > 30% the width of the blade 6
- 5b. Leaves entire to crenate, dentate or lobed, the lobes or teeth < 30% the width of the blade . . 8
 - 6a. Fruits linear; plants small (40 cm), erect, in open weedy lowland (0–600 m) sites; leaves opposite, to 20 mm long *Schistophragma mexicana*
 - 6b. Fruits broader; plants usually taller, in montane (1100–3800 m) habitats; leaves opposite or alternate, 10–100 mm long 7
 - 7a. Leaves opposite; corolla bright yellow with the lower lip sac-like; calyx 4-lobed, green *Calceolaria*
 - 7b. Leaves alternate; corolla and bracts red, orange, yellow, or green, the lower lip usually narrowed and with acute lobes; calyx 4-parted but usually united to form 2 large lateral lobes, often colored *Castilleja*
- 8a. (from 5b) Lower leaves alternate, plants usually with leaves alternate all along the stem 9
- 8b. Lower leaves opposite or whorled, distal leaves opposite or alternate along the stem or the leaves rosulate from the base 13
 - 9a. Corolla expanded at the base and spurred [yellow or blue, 5–30 mm long; lower leaves linear to lanceolate; cultivated for ornament] *Linaria*
 - 9b. Corolla tubular, not expanded at the base to become saccate or spurred; wild, naturalized, or cultivated species 10
- 10a. Plants repent with creeping stems rooting at most nodes; leaf blades rounded-orbicular [to 25 mm wide]; corolla 4–8-lobed, rotate, 3–5 mm wide *Sibthorpia repens*

- 10b. Plants erect, not rooting at distal nodes; leaf blades not rounded-suborbicular; corolla not rotate 11
- 11a. Corolla with the upper lip galeate, elongate, narrowly 1-lobed and entire, lower lip shorter than the upper, small and often recurved; distal bracts often becoming colorful [not found below 700 m elevation] *Castilleja*
- 11b. Corolla not as above, lobes rounded with the lower lobes usually longer than the upper; bracts not becoming colorful 12
- 12a. Corolla 7–10 mm long, white, campanulate; stamens 5; native plants at 0–500 m elevation. *Capraria biflora*
- 12b. Corolla 20–50 mm long, usually pink marked with purple dots within, tubular; stamens 4; in gardens or naturalized at 1800–3300 m elevation (if at lower elevations and with viscous hairs or slime glands, see Martyniaceae and Pedaliaceae) *Digitalis purpurea*
- 13a. (from 8b) Plants lacking erect stems, < 7 cm tall; found only in wet sites above 3300 m elevation in Central America; leaves linear to oblanceolate, in dense fascicles or rosulate at the nodes; corolla 2–3 mm long, rotate, with 3–5 lobes *Limosella acaulis*
- 13b. Plants with erect stems or without the above combination of characteristics 14
- 14a. Leaf blades linear to linear-lanceolate, often scabrous, larger blades not exceeding 7 mm in width [plants with stiff erect stems but rarely exceeding 0.7 m height; corollas 8–15 mm long] . . . 15
- 14b. Leaf blades narrowly lanceolate to broadly ovate or rounded, scabrous or smooth; larger blades usually > 7 mm in width 18
- 15a. Corolla 20–45 mm long or with spreading lobes to 2 cm wide, magenta, red, blue-violet, or purple to yellowish, glabrous or densely puberulent externally; flowers pedicellate in leaf axils or in distal racemes; plants not wiry or scabrous herbs or subshrubs, 0.4–1.5 m tall 16
- 15b. Corolla 7–15 mm long, lavender to pale purple, glabrous externally; flowers sessile or pedicellate; plants wiry and scabrous, herbs to 0.6 m tall 17
- 16a. Corolla densely minutely puberulent externally, narrowly tubular with small distal lobes *Lamourouxia* spp.
- 16b. Corolla glabrous externally, with short tube and broadly spreading large lobes *Angelonia angustifolia*
- 17a. Flowers borne on pedicels 10–35 mm long; fruits 4–7 mm diam.; erect stems usually with several prominent lateral branches *Anisantherina hispida*
- 17b. Flowers sessile or subsessile on pedicels < 3 mm long; fruits 2–3 mm diam.; erect stems usually with few or no prominent lateral branches *Buchnera weberbaueri*
- 18a. (from 14b) Corollas with the lower lip forming a distal sac and slipper-like, usually bright yellow [10–25 mm long; plants both wild and cultivated for ornament] *Calceolaria*
- 18b. Corollas not slipper-like, the lower lip not forming a distal sac, variously colored, usually with a short or long tube and spreading distal lobes 19
- 19a. Corollas becoming > 15 mm long at anthesis 20
- 19b. Corollas usually < 15 mm long at anthesis 29
- 20a. Corollas 70–120 mm long, white and salverform (with a narrow tube and broad subequal rotate lobes) *Escobedia grandiflora*
- 20b. Corollas 14–45 mm long, variously colored, usually tubular and somewhat 2-lipped with the lobes unequal 21
- 21a. Corolla yellow or yellow and white [flowers in axillary groupings; leaves sessile and auriculate at the base, blades narrowly lanceolate; native wild plants] 22
- 21b. Corolla pink to red or purple, marked with dark spots if white or yellowish (note that *Martynia* and *Sesamum* may key out in this dichotomy; see Martyniaceae and Pedaliaceae, Fig. 27) 24
- 22a. Plants weak-stemmed herbs to 0.4 m tall; leaves petiolate with blades rounded or truncate at the base; flowers solitary in leaf axils [corolla 14–20 mm long] *Mimulus glabratus*
- 22b. Plants erect subshrubs, often to 1 (2) m tall; leaves sessile with blades lanceolate and gradually narrowed to the base; flowers usually several in leaf axils 23

- 23a. Corolla 25–45 mm long, calyx 11–16 mm; fruits dry, brownish, oblong, 13–17 mm long *Hemichaena fruitcosa*
- 23b. Corolla 14–23 mm long, calyx 5–9 mm long; fruits fleshy, white, globose, 7–10 mm long *Leucocarpus perfoliatus*
- 24a. Corolla densely minutely puberulent or glandular puberulent on the exterior 25
- 24b. Corolla glabrous on the exterior 26
- 25a. Corollas densely minutely puberulent externally, the throat not closed by a palate; native wild species *Lamourouxia*
- 25b. Corollas sparsely puberulent, throat usually closed by a palate; cultivated ornamentals *Antirrhinum*
- 26a. Corolla tube ca. 2–4 mm diam., with small distal lobes, deep red; plants shrub-like ornamentals, often without leaves and with many slender green stems *Russelia equisetiformis*
- 26b. Corolla tube 7–10 mm diam., with prominent distal lobes, purple to rose-white or marked with dark coloring; plants not shrub-like, rarely without leaves 27
- 27a. Plants of wet forests; stems usually unbranched and < 30 cm tall; leaf blades oblanceolate, to 31 cm long *Tetranema*
- 27b. Plants of gardens and ornamental plantings; stems usually with a few branches, 0.4–1 m tall; leaf blades not oblanceolate, to 10 cm long 28
- 28a. Plants becoming ca. 1 m tall; calyx united for only a short distance, lobes > half the length of the calyx; staminode prominent; grown as ornamentals in Costa Rica *Penstemon gentianoides*
- 28b. Plants to 0.4 m tall; calyx united for half its length or more, lobes < half the length of the calyx; wild and ornamental species in Costa Rica *Torenia*
- 29a. (from 20b) Calyx united for > half its length at anthesis, a calyx tube clearly present (note that flowers may appear to have separate sepals after anthesis as the fruit develops and the calyx tube splits) 30
- 29b. Calyx with the sepals united only at the base, a calyx tube not evident 35
- 30a. Stems and leaves scabrid or hispid, stems often becoming 1 m tall; flowers sessile or subsessile in distal spike-like inflorescences 31
- 30b. Stems and leaves neither scabrid nor hispid, stems rarely > 40 cm tall; flowers not sessile in spike-like terminal inflorescences (except in *Bacopa sessiliflora*) 32
- 31a. Corolla yellow, campanulate; flowers subtended by large bracts differing little from the leaves; distal leaves narrowly triangular *Alectra aspera*
- 31b. Corolla white or marked with purple or blue, salverform; flowers subtended by bracts much smaller than the leaves; distal leaves narrowly lanceolate ... *Buchnera pusilla*
- 32a. Lower leaves forming a rosette, blades narrowly obovate with long-attenuate base; flowers in lax terminal racemes; rarely encountered introduced weeds *Mazus pumila*
- 32b. Lower leaves not forming dense rosettes, blades narrowly obovate to suborbicular; flowers mostly axillary to distal leaves 33
- 33a. Calyx 4-lobed; stems terete; leaf blades varying from obovate to suborbicular (rarely ovate with truncated base) *Bacopa egensis*
- 33b. Calyx 5-lobed; stems 4-angled or with 2–4 longitudinal ridges; leaf blades mostly ovate-triangular or ovate-ellipsoid with truncated base 34
- 34a. Calyx tube < 4 mm long, usually campanulate; fruits 3–4 mm long, rounded ovoid *Lindernia*
- 34b. Calyx tube usually > 7 mm long, tubular; fruits 8–10 mm long, narrowly ellipsoid-oblong *Torenia thourarsii*
- 35a. (From 29b) Fruits usually lenticular in cross-section, truncated or rounded and obcordate at the apex; stamens 2; corolla tube very short, with corolla lobes usually in a single plane (rotate); introduced weeds, 1000–3300 m elevation *Veronica*
- 35b. Fruits usually round in cross-section, never truncated or obcordate at the apex, and without the other combination of characteristics 36
- 36a. Sepals very unequal, the outer usually much broader than the inner and imbricate in bud (note that small linear bracteoles may be present at the base of the calyx) 37

- 36b. Sepals equal or subequal, valvate or less often imbricate in bud 38
 37a. Flowers yellow; bracteoles present at the base of the pedicel; leaf blades broad and abruptly narrowed to a short petiole *Mecardonia procumbens*
 37b. Flowers purple or blue to white (sometimes yellowish in age); bracteoles present in the middle or apex of the pedicel or absent; leaf blades usually gradually narrowed to the base or sessile if rounded at the base *Bacopa*
 38a. Corollas bright red or orange; plants erect herbs or subshrubs to 2 m tall, stems often stiff and longitudinally ridged 39
 38b. Corollas white to blue, purple, or yellowish; plants mostly weak-stemmed herbs 41
 39a. Leaf blades 15–31 cm long; corollas 26–55 mm long; peduncles 9–24 cm long, axillary, slender and flexuous; rarely collected endemic species *Tetranema*
 39b. Leaf blades 1–11 cm long; corollas 5–16 mm long; peduncles less than 2 cm long or the flowers on terminal erect racemes; common and widespread species 40
 40a. Flowers in axillary fascicles of 2–20, corolla deep red, tube 9–12 mm long with small acute lobes; seeds surrounded by hairs within the fruit *Russelia sarmentosa*
 40b. Flowers solitary in bract or leaf axils on a terminal raceme, corolla red to orange, tube < 2 mm long with large rounded spreading-rotate lobes; seeds not associated with hair-like structures *Alonsoa meridionalis*
 41a. Corolla < 4 mm long, rotate or campanulate 42
 41b. Corolla 4–14 mm long, usually tubular and bilabiate 43
 42a. Plants terrestrial, erect, to 1 m tall; leaf blades to 35 mm long, oblanceolate and dentate; fertile stamens 4 *Scoparia*
 42b. Plants floating or prostrate, small; leaves to 8 mm long, rounded and entire; fertile stamens 2 *Micranthemum umbrosum*
 43a. Fertile stamens 2; leaves sessile; stems glabrous *Lindernia dubia*
 43b. Fertile stamens 4; leaves petiolate (sessile and amplexicaul in *Stemodia durantifolia*); stems glabrous or puberulent 44
 44a. Anthers glabrous; stems and leaves puberulent; sepals acute at the apex *Stemodia*
 44b. Anthers with hairs; stems and leaves glabrous; sepals bluntly acute and often thickened at the apex *Darcya*

Agalinis Rafinesque
 Nomen conservandum

Herbs or shrubs, annual or perennial, usually erect and branched, glabrous or pubescent, hemiparasitic on roots, turning dark when dried. **Leaves** opposite or alternate, becoming smaller or bract-like on distal stems, subsessile or sessile, blades usually narrow, entire or lobed, glabrous or puberulent. **Inflorescences** of solitary flowers in axils of reduced distal leaves (often resembling open racemes, spikes, or panicles), peduncles slender, subtended by small bracts, pedicels slender, bibracteolate or ebracteolate. **Flowers** showy, calyx tubular to campanulate or hemispheric, with 5 prominent lobes or teeth, slightly imbricate or open in bud; **corolla** campanulate and often somewhat bilabiate, glabrous or puberulent, pink to purple (yellow or white), tube straight or curved, expanded distally into a broad throat, lobes 5, rounded, subequal or the posterior (upper) smaller; **stamens** 4, of 2 unequal pairs, borne from the

middle of the corolla tube, shorter than the corolla, filaments usually pilose, anthers glabrous or puberulent, 2-thecous with parallel thecae, unequal in some species; ovary glabrous, 2-locular, style straight and slender, deciduous, stigma solitary and linear. **Fruits** rounded capsules, woody to chartaceous or leathery, dehiscence loculicidal (and sometimes septicidal); seeds many, oblong to angular, testa reticulate.

A distinctive New World genus with ca. 40, mostly North American, species. Species of this genus were formerly placed in *Gerardia*, but the Linnaean type proved to be a species of Acanthaceae. This genus has not been collected in Costa Rica, but ranges southward as far as northern Nicaragua. The following key includes *Anisantherina hispidula*, which occurs in Costa Rica (q.v.), and two species of *Agalinis* known from Nicaragua: *Agalinis albida* Britton & Pennell (? = *Agalinis harperi* Pennell) and *Agalinis peduncularis* (Benth.) Pennell. All three species have linear leaves.

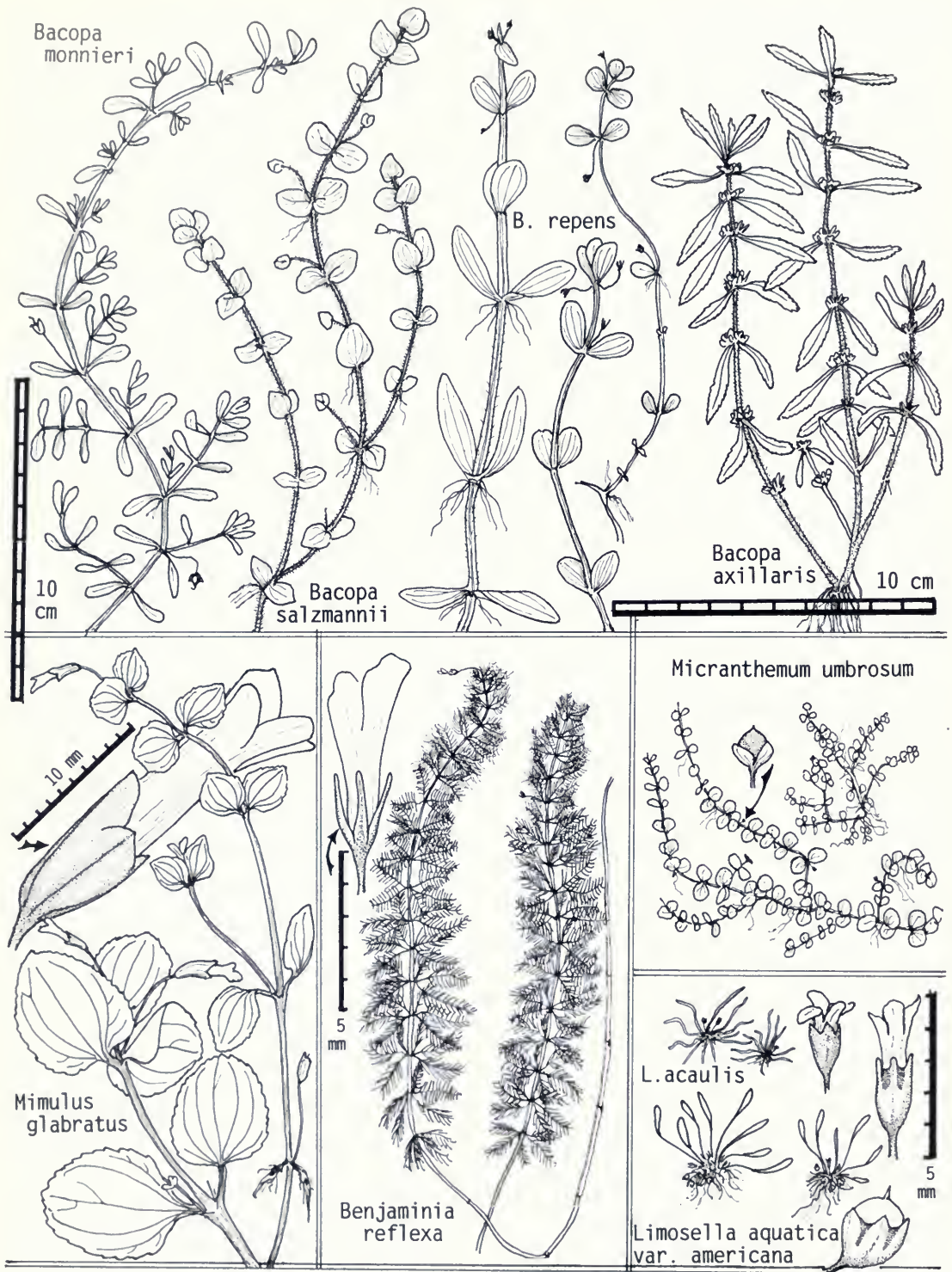


FIG. 1. Scrophulariaceae: aquatic and semiaquatic species.



FIG. 2. Scrophulariaceae: small herbs with opposite leaves and broad blades.

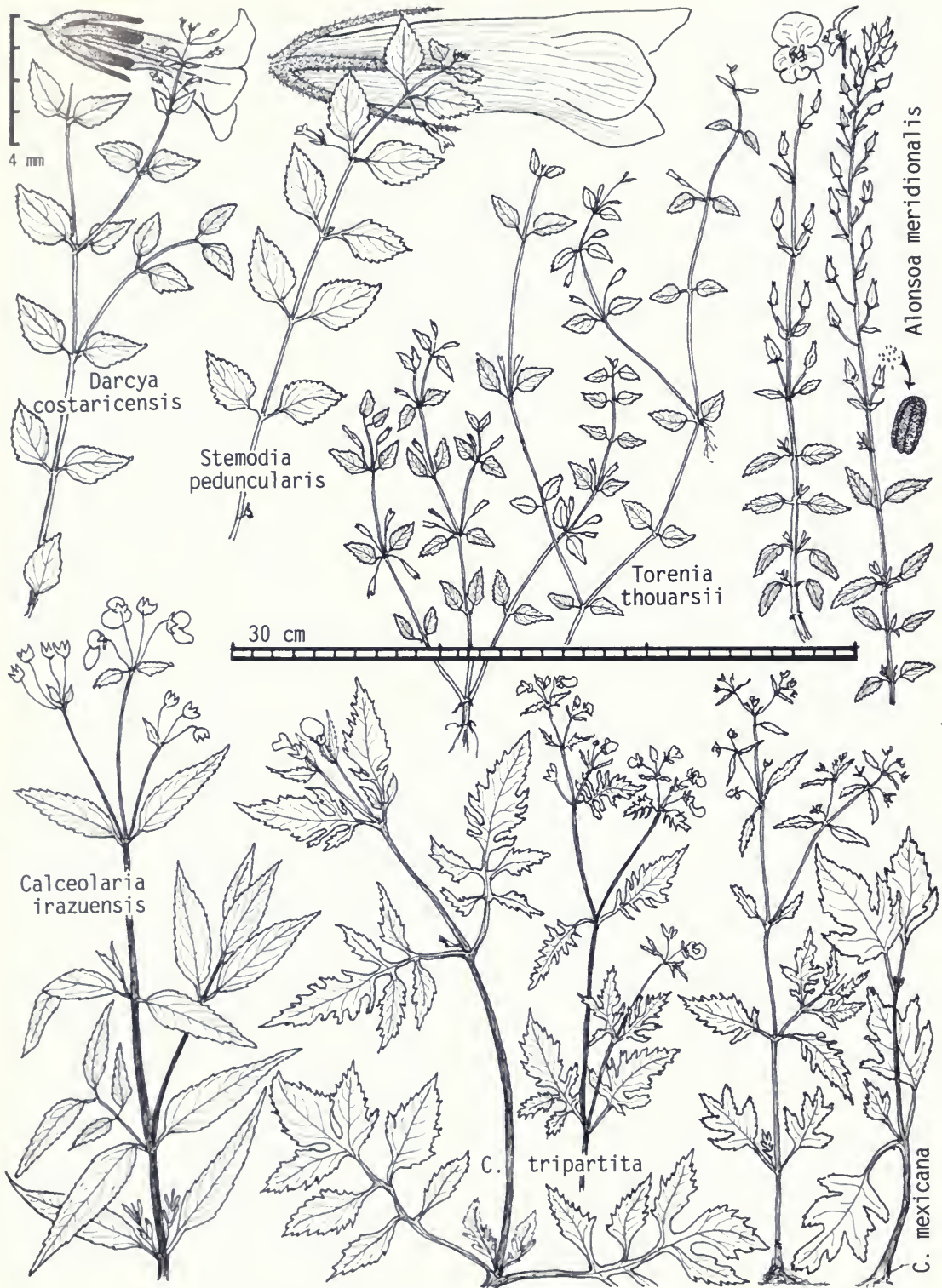


FIG. 3. Scrophulariaceae: herbs with opposite leaves and lanceolate to ovate or dissected blades.



FIG. 4. Scrophulariaceae: herbs with opposite leaves and narrow leaf blades or narrow pinnatifid lobes.



FIG. 5. Scrophulariaceae: herbs with stiff opposite leaves and erect or clambering stems.

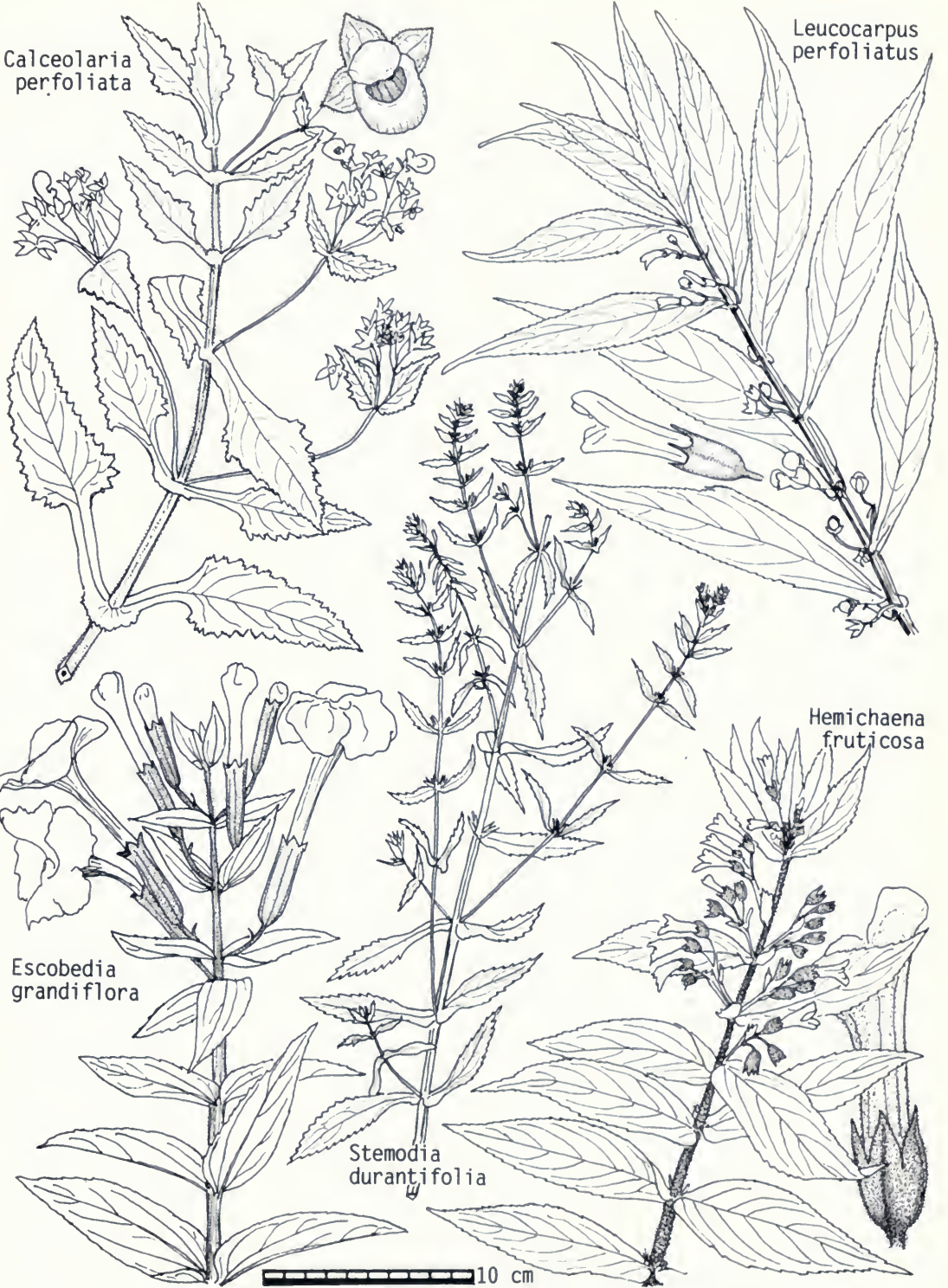


FIG. 6. Scrophulariaceae: erect herbs with larger sessile or perfoliate leaves.

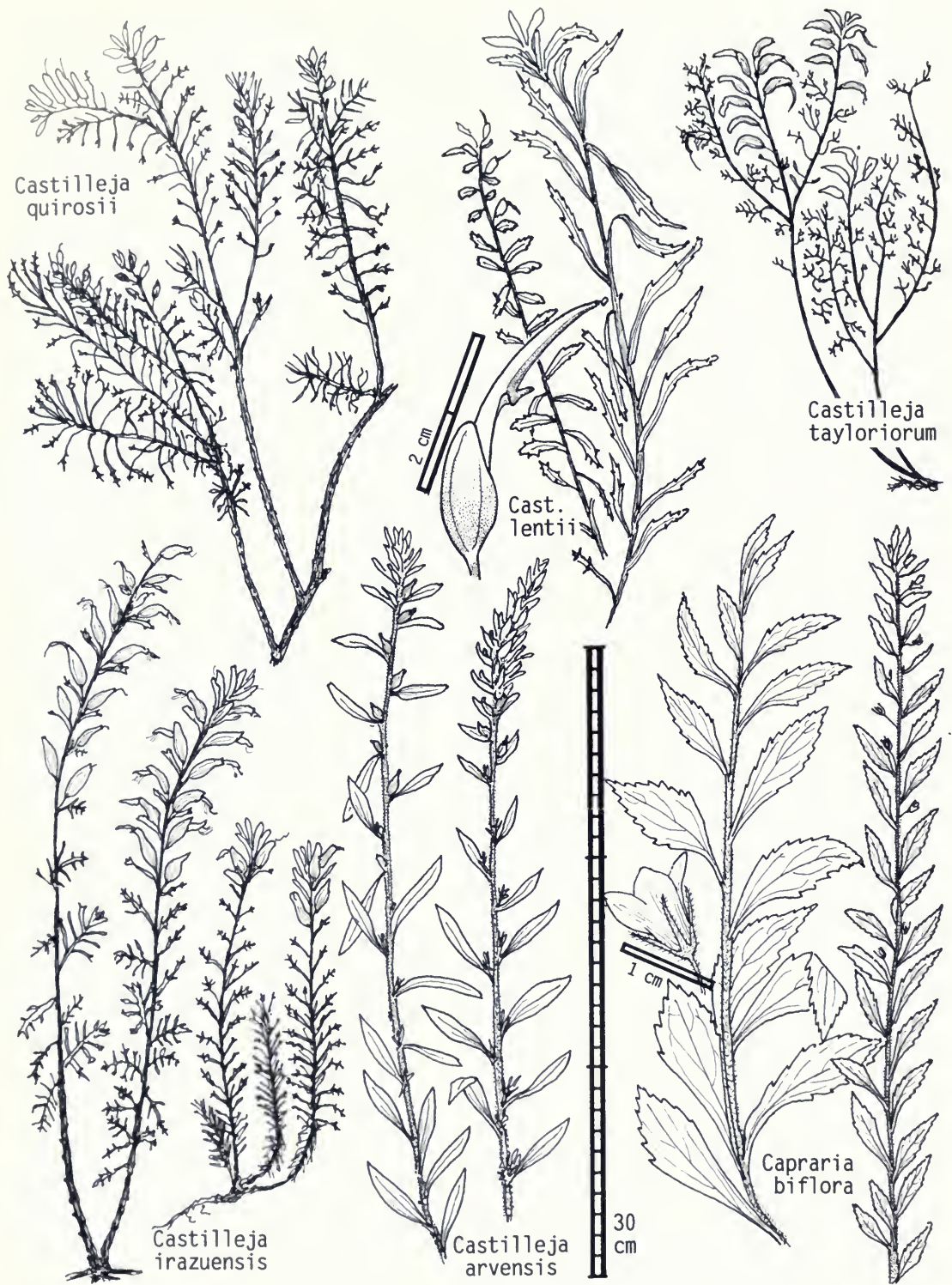


FIG. 7. Scrophulariaceae: erect herbs with consistently alternate leaves and unusual curved flowers (*Castilleja*) or simple, almost regular flowers (*Capraria*).

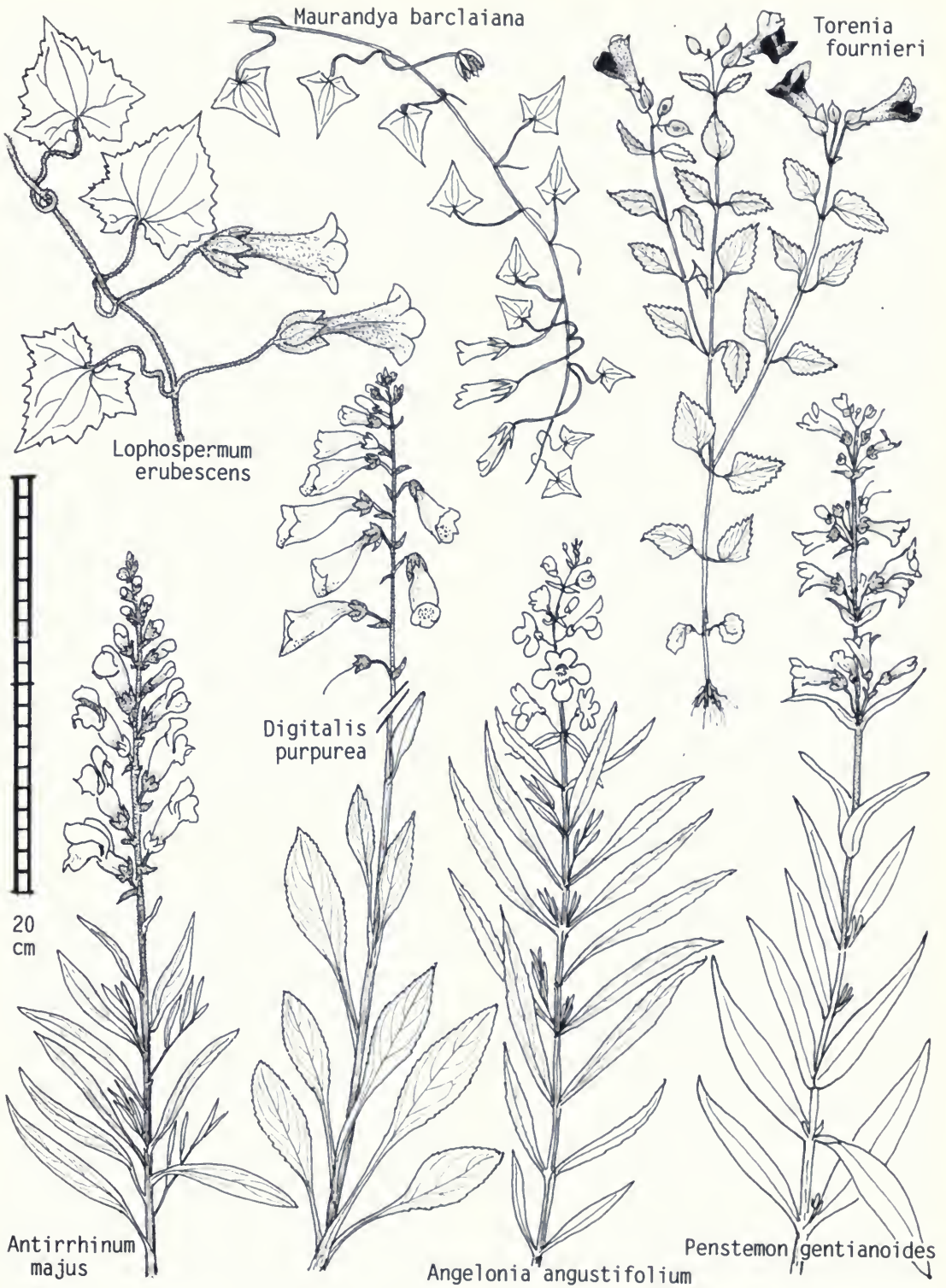


FIG. 8. Serophulariaceae: wild and cultivated species with large colorful corollas and alternate or opposite leaves.

Key to Species of *Agalinis* and *Anisantherina*

- 1a. Flowers usually 1/node, pedicels shorter than the calyx; distal leaves mostly alternate; stems and leaves smooth to the touch *Agalinis albida*
- 1b. Flowers usually 2/node, pedicels much longer than the calyx; distal leaves mostly opposite or subopposite; stems and leaves slightly scabrous 2
- 2a. Corolla 20–30 mm long, edge of corolla lobes with multicellular hairs; anther thecae equal in size and shape; calyx lobes narrow; pedicels without nodes or bracts *Agalinis peduncularis*
- 2b. Corolla 10–16 mm long, edge of corolla lobes glabrous; anther thecae slightly unequal in size and shape; calyx lobes triangular; pedicels usually with a node or bracts (reduced leaves) near the middle *Anisantherina hispidula*

Alectra Thunberg nomen conservandum

REFERENCE—H. Melchior, Die Gattung *Alectra* Thunb. Notizbl. Bot. Gart. Berlin 15: 423–447. 1941.

Erect annual **herbs**, hemiparasitic, turning dark when dried, unbranched to few-branched, with hispid or scabrous hairs often enlarged at the base. **Leaves** opposite or subopposite (or alternate above), reduced in size distally (rarely absent), simple and sessile or subsessile, margins serrate to dentate (entire), often with 3 prominent veins from the base. **Inflorescences** racemose or spicate, elongate, of solitary flowers in axils of distal leaves, pedicels (peduncles) short, with 2 (1) distal bracts or bracts absent. **Flowers** with campanulate calyx, 10-veined, persisting and enclosing the fruit, with 5 acute to obtuse lobes, valvate in bud, equaling the tube in length; **corolla** usually yellow or orange, personate to subglobose or campanulate, as long or slightly longer than the calyx, 5-lobed and slightly bilabiate, lobes rounded, shorter or equaling the tube; **stamens** of 2 shorter and 2 longer pairs, attached near the base of the corolla, included, filaments glabrous or puberulent, anthers 2-thecous, often barbate abaxially, disc annular and fleshy; **ovary** ovate or compressed, 2-locular with thick fleshy placenta and many seeds, style linear, elongate, and inflexed, stigma entire or bifid, thickened. **Fruits** loculicidal capsules enclosed within the dry calyx, rounded or compressed; seeds very numerous, small, with transparent exotesta often truncated and open at the 2 ends.

A genus of 41 species, according to Melchior (1941, above). Nearly all the species are from Africa and India. The one American species is native to South America and the West Indies; it differs from the Old World species in having divergent

rather than parallel anther thecae. *Alectra* is closely related to *Melasma* in the tribe Buchnereae and was once united with that genus. Few characters reliably distinguish the two. In *Melasma* the corolla is twice as long as the calyx and is more campanulate than that of *Alectra*.

Alectra aspera (Cham. & Schldl.) L. O. Williams, Fieldiana, Bot. 34: 118. 1972. *Pedicularis melampyroides* L. C. Rich., Actes Soc. Hist. Nat. Paris 1: 111. 1792. *Glossostylis aspera* Cham. & Schldl., Linnaea 3: 22. 1828. *Scrophularia fluminensis* Vell., Fl. flumin., 263. 1829. *A. brasiliensis* Benth. in DC., Prodr. 10: 339. 1846. *A. melampyroides* (L. C. Rich.) Kuntze, Rev. Gen. Pl. 2: 458. 1891, non *A. melampyroides* Benth. 1846. *Melasma melampyroides* (L. C. Rich.) Pennell in Britton & Wilson, Bot. Porto Rico 6: 188. 1925. *A. fluminensis* (Vell.) Stearn, J. Arnold Arbor. 52: 636. 1971. Figure 5.

Herbs 0.3–1.5 m tall, stems erect and simple to many-branched, main stems 1.7–6 mm diam., scabrid with straight stiff whitish hairs 0.3–1.5 mm long, short (0.1–0.2 mm) thin hairs also present. **Leaves** becoming gradually smaller distally, opposite, subopposite (rarely alternate distally), subsessile with petioles 0.5–4 mm long; **leaf blades** 1–5(–7) cm long, 4–16(–25) mm wide, narrowly ovate-triangular to ovate-lanceolate or lanceolate, gradually narrowed to the acute or acuminate apex, margin coarsely serrate with teeth 0.3–2.5 mm high, base truncated or obtuse, surfaces scabrous with stiff whitish hairs 0.1–0.9 mm long, venation subpalmate with midvein and 2 prominent ascending basal 2° veins (tripliveined). **Inflorescences** of spike-like or raceme-like distal stems or with solitary flowers in the axils of smaller leaves (1–2 flowers/node), pedicels 1–2(–7) mm long, ca. 0.5 mm diam., bracts linear

or absent, at the base of the calyx, ca. 3 mm long. **Flowers** with campanulate calyx 6–9 mm long (to 12 mm in fruit), 5–8 mm wide at the mouth, calyx lobes 2–6 mm long, triangular and acute, with scabrous hairs along the margins and veins; **corolla** 10–13 mm long, included within the calyx or slightly exerted, campanulate, yellow, glabrous, tube 5–8 mm long, lobes subequal; stamens with pubescent filaments, anthers 1.5 mm long, thecae divergent, without awns; ovary ca. 3 mm long, ovoid, style 6–8 mm long, curved, stigma lanceolate. **Fruits** 5–8 mm long, 4–6 mm diam., oblate-globose, included within the persisting calyx; seeds 1–1.2 mm long, oblong-triangular with truncated ends, translucent yellowish, exotesta reticulate.

Weeds of open sunny sites in lowland Central America. It is a recent introduction and is spreading. It has been collected near Upala and Villa Neilly, at Tarrazu, and on the lower slopes of the Cerros de Puriscal. The species ranges from Guatemala and the West Indies to Brazil, Paraguay, and Bolivia.

Alectra aspera is recognized by its short erect stems, stiff pustulate-hispid leaves, tissues drying dark, solitary flowers in distal leaf axils, corolla tube only as long as the calyx, persisting campanulate-globose calyx, and minute seeds with translucent testa. The corolla of this species is open for a very short time. It soon withers, closing over the anthers and the stigma. The anthers are borne close to the stigma, suggesting that the species is largely self-pollinating.

Alonsoa Ruíz López & Pavón

REFERENCES—J. López Guillén, El Genero *Alonsoa* en el Peru: 1. Revision de las especies endemicas. Raymondiana 3: 155–246. 1970 (1971). Brian Wrigley, A taxonomic revision of *Alonsoa*. Ph.D. diss., Univ. Connecticut, 1968.

Herbs or subshrubs, annual or perennial, often with distal branching, usually woody at the base, stems quadrangular in cross-section, glabrous or sparsely minutely puberulent. **Leaves** opposite or ternate (leaf-like floral bracts alternate), sessile or petiolate, leaf blades ovate to linear, serrate or rarely entire, venation pinnate. **Inflorescences** racemes, terminal or axillary to distal leaves (rarely flowers axillary to distal leaf pairs), floral bracts alternate along the rachis, proximal bracts leaf-like, pedicels solitary, well developed, and becoming twisted, bracteoles absent. **Flowers** small,

resupinate because of pedicel twisting, calyx deeply 5-parted, lobes narrow and slightly unequal, glabrous or sparsely and minutely puberulent, valvate in bud; **corolla** rotate with very short tube, bilaterally symmetric with the 2 lower lobes small and divided nearly to the base, lateral lobes short and broad, upper lobe much larger and usually held erect and convex, reddish to orange or purple; stamens 4, subequal, borne on the base of the corolla, filaments thick or slender, anthers closely positioned around the style, thecae parallel or divergent; ovary 2-locular, style curved upward, stigma capitate. **Fruits** capsules, ovate to oblong, septicidal, 2-valved, valves chartaceous, entire or bifid at the apex; seeds many, punctate-rugose or longitudinally ridged.

Alonsoa is a Neotropical genus of six to fifteen species. The flowers are upside-down (resupinate) because of the twisted pedicel, with the result that the morphologically lower lobe is the upper lobe. The reddish to yellow resupinate flowers with enlarged median lobe are distinctive. The genus is placed in the tribe Hemimeridae, with *Angelonia*, but is probably more closely related to *Scrophularia* and *Verbascum*, with which it shares characters of seed and anther morphology. *Alonsoa warscewiczii* Regel is often used as a potted ornamental plant; only one species is found in the higher mountains of Central America. The genus is currently being studied by Fanny Astholm (GB).

Alonsoa meridionalis (L.f.) Kuntze, Rev. Gen. Pl. 2: 457. 1891.

Scrophularia meridionalis L.f., Suppl. 280. 1781. Figure 3.

REFERENCE—F. Astholm & Y. Nyman, Morphometric variation in the *Alonsoa meridionalis* complex (Scrophulariaceae). Plant Syst. Evol. 193: 53–68. 1994.

Herbs or subshrubs 0.2–1.5 m tall, often woody at the base, usually with lateral branches, leafy stems 0.7–8 mm diam., glabrous or sparsely minutely puberulent (rarely densely puberulent at the node), with 4 prominent longitudinal ridges or wings (from decurrent petiole margins). **Leaves** opposite (sometimes alternate below the flowering nodes), petioles 3–15(–22) mm long, 0.4–1.7 mm diam., glabrous or with few hairs less than 0.3 mm long, with lateral margins continuous with the blade margins; **leaf blades** 1.5–8(–11) cm long,

1–4 cm wide, ovate-lanceolate to oblong-lanceolate or narrowly ovate, apex acute, margin with 4–7 acute teeth/cm, base obtuse to slightly cuneate and decurrent, drying greenish or dark, sparsely puberulent on both surfaces, 2° veins 5–10/side, strongly ascending. **Inflorescences** terminal racemes 3–30 cm long, flowers opposite or distally alternate, subtended by progressively smaller, leaf-like to subulate bracts 4–14 mm long, pedicels 6–18(–25) mm long, glabrous or with few minute (0.2 mm) gland-tipped hairs, upcurved in fruit. **Flowers** resupinate, calyx 3–6 mm long, divided to near the base, lobes 1–1.7 mm wide, subequal or unequal, glabrous or with few minute hairs near the base; **corolla** 5–11 mm long, rotate, yellow to orange, tube ca. 2 mm long, with prominent lobes, median lobe to 15 mm long, larger than the lateral lobes; stamens 3–4 mm long, filaments 0.4–0.6 mm diam., anthers ca. 2 mm long; ovary 1.5–4 mm long, narrowly ovoid, style 1.5–2 mm long, stigma 0.8 mm wide. **Fruits** 7–15 mm long, 3.7–6 mm wide, narrowly ovoid with acute to acuminate apex, smooth, glabrous, pale brown, sulcate along the plane of dehiscence, septicidal; seeds many, 1.1–1.4 mm long, 1–1.2 mm diam., oblong, dark, with ca. 6 deep longitudinal sulci.

Plants of open sites in high montane forest formations, 1600–3200 m elevation. Flowering in October–December. In Costa Rica they are found in the Cordillera Central and the Cordillera de Talamanca. The species ranges from southern Mexico to Bolivia.

Alonsoa meridionalis is recognized by its terminal racemes with solitary, usually alternate flowers subtended by bracts gradually diminishing in size, unusual little flowers with red-orange corolla with enlarged median uppermost lobe, short thick filaments, large anthers, and capsules gradually narrowed to the apex. Because the pedicels are twisted 180°, the flowers are upside-down (resupinate). The leaves often have new shoots with small leaves in their axils.

Angelonia Humboldt & Bonpland

REFERENCE—K. Barringer, A Revision of *Angelonia* (Scrophulariaceae). Ph.D. diss. Univ. Connecticut, 1981.

Erect **herbs** or shrubs, annual or perennial, stems terete to 4-angulate, simple or branching from the base, puberulent with multicellular hairs or glabrous. **Leaves** opposite or rarely alternate distally, petioles short or absent; blades ovate to

linear, serrate or rarely entire, apex acute, venation pinnate. **Inflorescences** racemes, terminal or axillary, bracts leaf-like to rounded, flowers 1–3/axil, pedicels bibracteolate or ebracteolate. **Flowers** showy, calyx of 5 free or partly united sepals, sepals equal, lanceolate, entire, acute to acuminate; **corolla** strongly bilaterally symmetric, cupular-campanulate with short tube and 2 broadly flaring lips, bisaccate at the base of the median lobe, the sacs with a dense mat of glandular hairs within, lobes 5, upper lobes 2, the lower median (abaxial) lip 3-lobed, variously ornamented with a ridge or a crateriform palate and a bifid tooth; **stamens** 4, of 2 unequal pairs, held against the upper part of the corolla tube, filaments short, thecae divaricate, without spurs; ovary ovoid, 2-locular, ovules many, style longer than the ovary, stigma entire and minute. **Fruits** dry capsules, ovoid to broadly ellipsoid, chartaceous or leathery, septicidal, often secondarily loculicidal; seeds many, obconical, with a loose reticulate exotesta, endosperm absent.

A genus of 26 species whose major concentration is in the dry caatinga and cerrado formations of Brazil. The Central American and Caribbean species form a distinctive group within the genus. The genus is easily distinguished by the bisaccate corolla and the ornamented median corolla lobe. One species is found in Costa Rica; a second, *Angelonia ciliaris* B. L. Robinson (with puberulent leaves auriculate at the base), ranges from southern Mexico and the Antilles to Nicaragua.

Angelonia angustifolia Benth. *in DC.*, Prodr. 10: 254. 1846. Figure 8.

Herbs 20–120 cm tall, erect, few-branched or unbranched, leafy stems 1.5–5 mm diam., terete or slightly 4-angled, sparsely puberulent with thin multicellular hairs 0.5–2 mm long at the nodes or along longitudinal lines. **Leaves** becoming smaller distally (intergrading with the floral bracts), opposite or subopposite, sessile or subsessile, often clasping the stem; **leaf blades** 2–11 cm long, 4–20 mm wide, linear to narrowly elliptic-oblong or lanceolate, apex acute, margin obscurely serrate with short (0.2–0.6 mm) teeth 1–4/cm, base cuneate to acute, drying chartaceous and brown or dark grayish green, surfaces subglabrous with few thin hairs, 2° veins 3–6/side and strongly ascending. **Inflorescences** 5–40 cm long, flowers solitary in distal leaf/bract axils (usually 2/node), pedicels 4–18 mm long, 0.2–0.4 mm diam., glabrous, ascending, subtended by 2 linear bracteoles 0.5–2 mm long. **Flowers** glabrous, calyx 2–4 mm

long, 1–2 mm wide at the base, narrowly ovoid to campanulate, calyx lobes 2–3.5 mm long, lanceolate to triangular; **corolla** 8–25 mm wide at the mouth, purple to lavender or bluish, minutely punctate, tube white to yellowish or green, often marked with white on the palate (basal entry of the throat), corolla lobes to 9 mm long, rounded; stamens included, filaments glandular-pubescent, anthers 2 mm wide, thecae divergent, equal, glabrous; ovary glabrous. **Fruits** 4–6 mm long, 4–7 mm diam., globose to ovoid-rounded with truncated base, glabrous; seeds 1.3–1.5 mm long, conic to oblong, exotesta strongly reticulated with prominent thin walls.

Native to southern Mexico, this species has spread into much of Central America, where it is a favorite garden ornamental. In Costa Rica it has been collected in both the deciduous and evergreen lowlands and from gardens in the Meseta Central; it flowers throughout the year. The species is now cultivated throughout the world.

Angelonia angustifolia is recognized by its small stature, narrow subglabrous opposite leaves, showy corolla with prominent spreading rounded lobes, and unusual seed surface. This species is probably pollinated by *Centris* bees, which collect a thick oil from the corolla sacs with specialized combs on their front legs. Common names used for this species are *boca de la vieja* (Guatemala), *porto bello* (Nicaragua), and *angelón* (Colombia).

Anisantherina Pennell

Herbs, annual, erect with ascending branches, hispidulous with multicellular hairs with dark cross-walls, hemiparasitic on roots, turning dark when dried. **Leaves** opposite or subopposite distally, becoming smaller or bract-like on distal stems, sessile, blades linear and entire, scabrous. **Inflorescences** of solitary flowers in the axils of reduced distal leaves (raceme-like with well-separated flowers), pedicels often longer than the calyx, bibracteolate. **Flowers** showy, calyx campanulate with 5 prominent equal lobes; corolla tubular-campanulate, slightly bilabiate, glabrous, pink to purple, tube straight or curved, expanded distally into a broad throat, 2-lipped, upper lip 2-lobed, lower lip 3-lobed, lobes rounded, subequal, spreading; **stamens** 4, of 2 unequal pairs, inserted near the mouth of the corolla tube, shorter than the corolla, anterior filaments longer than the posterior, pilose above, anthers 2-theccous with unequal divergent thecae, glabrous; ovary ovoid, glabrous, 2-locular, style longer than the ovary,

straight and slender, stigmas linear and lateral on the liguliform style apex. **Fruits** globose capsules, chartaceous, loculicidal, style base persistent, placentae persistent; seeds many, linear, exotesta reticulate.

Anisantherina is a monotypic Neotropical genus related to African genera in the tribe Buchnereae. Pennell distinguished *Anisantherina* from *Agalinis* by its bibracteolate pedicels, unequal anther thecae, and narrow oblong-linear seeds. Canne (1980) showed that the structure and ornamentation of *Anisantherina* seeds are also distinctive. This species was once placed in *Gerardia*, but that name is no longer valid; see the discussion under *Agalinis*.

Anisantherina hispidula (Mart.) Pennell, Mem. Torrey Bot. Club 16: 106. 1920. *Gerardia hispidula* Mart., Nov. Gen. Sp. Pl. 3: 13. 1829. *Agalinis hispidula* (Mart.) D'Arcy, Ann. Missouri Bot. Gard. 65: 4. 1978 (1979). Figure 4.

Annual **herbs**, 30–50 cm tall, unbranched or with few branches arising in the lower half, leafy internodes 0.5–1.5 mm diam., with few short (0.2–0.4 mm) stiff hispidulous hairs; usually drying dark. **Leaves** opposite or subopposite (rarely alternate distally), sessile or subsessile, sometimes clasping the stem; **leaf blades** 8–80 mm long, 0.5–4 mm wide, linear, entire, scabrous with short (ca. 0.2 mm) whitish hairs above and along the margin, 2° veins obscure. **Inflorescences** of solitary flowers in axils of reduced distal leaves, raceme-like with 8–14 flowers, pedicels 10–35 mm long, 0.3–0.4 mm diam., glabrous, usually with a node or a pair of small (0–2 mm) bracts near the middle. **Flowers** glabrous, drying dark, calyx tube 4–6 mm long, 3–5 mm diam., campanulate-tubular, abruptly rounded and truncated at the base, calyx lobes 1.2–2.5 mm long, triangular and acute; **corolla** 10–15 mm long, campanulate, pink to light purple with darker spots within, tube 8–10 mm long, lobes 2–3 mm long, glabrous, rounded; filaments 2–3 mm long, anther thecae unequal, divergent. **Fruits** 5–9 mm long, 4–7 mm diam., abruptly rounded at apex and base (short-cupulate), glabrous, drying black, slightly exerted beyond the thin persisting calyx; seeds 0.6–0.8 mm long, 0.2–0.3 mm diam., linear, dark brown.

Rarely collected plants of open sunny seasonal pools and moist savannas in deciduous or evergreen forest areas, 0–600 m elevation. We have seen only two collections from Costa Rica, both from near La Cruz in northern Guanacaste (*L. D. Gomez 18965* & *J. Gomez-Laurito 9097*); flow-

ering and fruiting in November. The species ranges from southern Mexico and Cuba to Brazil.

Anisantherina hispidula is recognized by its short wiry habit, parts drying dark, linear scarious leaves, glabrous distant upright pink flowers, and rounded fruits. It is confined to wet habitats in open sunny savannas. See the key and discussion under *Agalinis*.

Antirrhinum Linnaeus

REFERENCE—D. Sutton, A Revision of the Tribe Antirrhineae. British Museum (Natural History) & Oxford Univ. Press, 1988.

Herbs, annual or perennial, erect or procumbent, usually few-branched, stems terete, often glandular pubescent. **Leaves** opposite to subopposite, sometimes alternate on distal stems, sessile or short-petiolate, leaf blades lanceolate to ovate, usually narrow, entire to denticulate. **Inflorescences** usually showy terminal racemes or with solitary flowers in axils of distal bracts or reduced leaves, pedicels ebracteolate. **Flowers** with calyx united at the base, sepals 5, imbricate in bud; **corolla** bilaterally symmetric, 2-lipped and very irregular, corolla tube gibbous or saccate at the base (not spurred), broader than high, upper lip erect and 2-lobed, lower lip spreading and 3-lobed, base of the lower lobe forming a palate and pressing against the front of the throat (closing off easy entrance to the tube); **stamens** 4, of 2 unequal pairs, included in the corolla tube, filaments slender and slightly dilated at the apex, anther cells divergent, staminode absent; ovary ovoid, 2-locular, many-ovulate, style filiform, longer than the ovary, stigma bilobed. **Fruits** ovoid or globose capsules, opening below the apex by pores or slits (septicidal); seeds many, oblong, truncated, exotesta smooth or rugose (without wings).

A genus of about 42 species from the western United States, northwestern Mexico, Europe, and the Mediterranean region of Eurasia. The genus is a member of tribe Antirrhineae, with *Cymbalaria* and *Linaria*. A number of species and many varieties have been developed as garden ornamentals with bright red, purple, yellow, or white forms. The mouth of the corolla is closed by the curved palate of the lower lip, which is held against the base of the upper lip. Thus, bees must force their way into the interior of the corolla to gain access to nectar. The following species is commonly cultivated in cool highland gardens throughout Central America.

Antirrhinum majus L., Sp. Pl. 617. 1753. Figure 8.

Herbs, erect, 0.4–1 m tall, leafy stems 2–8 mm diam., glabrous and terete. **Leaves** opposite or ternate below, alternate or rarely ternate distally, petioles 1–14 mm long but poorly differentiated from the blade; **leaf blades** 2–9 cm long, 3–16 mm wide, lanceolate to ovate-lanceolate or linear, apex acute, margin entire, base gradually narrowed, drying stiffly chartaceous and greenish. **Inflorescences** to 30 cm long, racemes of alternate flowers, rachis usually densely puberulent with gland-tipped hairs ca. 0.3 mm long, bracts ovate, 2–10 mm long, acute, pedicels 2–10 mm long. **Flowers** showy, calyx glandular puberulent, sepals 5, 6–8 mm long, ovate to rounded; **corolla** 2.5–4 cm long, pink to red or purple, externally glandular hairy, the palate closing the throat, yellow within. **Fruits** 1–1.5 cm long, oblong capsules with unequal valves, opening near the apex, glandular pubescent to glabrous; seeds light brown, reticulate-tuberculate.

Antirrhinum majus is a native of the Pyrenees of northern Spain and southern France. It is widely cultivated in temperate and subtropical regions. It can be recognized by its showy racemes and slightly saccate corolla with an enlarged palate that “closes” the throat. In some horticultural forms the throat is open or the flowers are highly modified. Common names are “snapdragon,” *boca de león*, and *boca de dragón*.

Bacopa Aublet

REFERENCE—F. W. Pennell, Reconsideration of the *Bacopa-Herpestis* problem of the Scrophulariaceae. Proc. Acad. Nat. Sci. Philadelphia 98: 83–98. 1946.

Herbs, erect to decumbent or procumbent, usually growing in moist soil or in standing water, stems simple or profusely branched, glabrous or pubescent, often glandular punctate. **Leaves** opposite, sessile or petiolate, leaf blades often slightly succulent, entire to dentate (or dissected), venation pinnate or palmate, the minor venation usually obscure. **Inflorescences** of 1–6 flowers in leaf axils, less often the distal flowering stems racemose or spicate (cymose, paniculate), pedicels short or absent, bracteoles present or absent at the base of the calyx. **Flowers** usually with 5-parted calyx, sepals subequal to strongly unequal with the 3 adaxial sepals usually much wider than the

abaxial, imbricate in bud (if 4-parted, the calyx tube equaling the lobes); **corolla** tubular, strongly or weakly bilabiate, blue-violet to white, tube cylindrical, the lips spreading, with 3, 4, or 5 lobes, the upper lip exterior in bud and 2-lobed or emarginate (1-lobed), the lower lip 2- or 3-lobed; stamens (5) 4 (2, 3), usually in 2 unequal pairs, inserted on the upper half of the corolla tube, included, anthers approximate or distant, thecae contiguous, parallel or divergent, staminode absent; ovary 2-locular, style usually straight, stigma terminal, bilobed or entire. **Fruits** dry capsules, globose to ovoid, bisulcate, loculicidal, often secondarily septicidal into 4 valves; seeds many, small, oblong, longitudinally reticulate.

Bacopa is a genus of about 50 to 60 species, widespread in warm temperate and tropical areas

throughout the world. It is most diverse in South America. The species are varied but they can usually be recognized by their small opposite leaves, strongly unequal sepals, and preference for wet habitats. They are often found in open sunny sites in shallow standing water of seasonal pools, along the edges of watercourses, and in moist savannas. Most of the species described below are rarely collected in Costa Rica, perhaps because of their seasonally inundated habitats. Because the sepals differ so much in size, they may appear to be bracts enclosing the flower. The inner sepals are usually much narrower than the outer. The bracteoles are borne at the apex of the pedicel when present. The synonymy of this genus is very large; D'Arcy (1979, p. 183) provides a long list of generic synonyms.

Key to the Species of *Bacopa*

- 1a. Flowers sessile or subsessile, pedicels up to 2 mm long; plants erect; rarely collected in Costa Rica 2
- 1b. Flowers borne on conspicuous pedicels > 2 mm long; plants erect, prostrate or floating; rare or common 4
 - 2a. Stems densely puberulent with hairs to 1.3 mm long; [flowers often in dense verticels of 3–12 flowers/node in the axils of leaves; outer calyx lobes 3–4 mm long] *B. axillaris*
 - 2b. Stems glabrous or minutely puberulent, the hairs < 0.5 mm long 3
 - 3a. Stems puberulent; fruits with smooth surfaces; outer sepals 1–2 mm long; flowers in distal fascicles separated by conspicuous slender internodes; leaves subtire ... *B. monnieroides*
 - 3b. Stems glabrous; fruits with pitted-reticulated surfaces; outer sepals 2–3.5 mm long; flowers often in distal crowded fascicles and spike-like with obscure internodes; leaves serrate *B. sessiliflora*
- 4a. Plants mostly erect with few to many distal branches, rooting only at the base, stems glabrous, leaves serrate, sessile and auriculate at the base (petiolate in *B. lacertosa*), opposing leaves not united and usually without an interpetiolar line 5
- 4b. Plants usually prostrate, floating or creeping, with few or no distal branches, rooting at base and lower nodes, stems glabrous or puberulent; leaves serrate or entire, sessile or petiolate, opposing leaves slightly united across the stem to form an interpetiolar line or ridge or the node pubescent 7
 - 5a. Outer sepals to 5 mm long, sepals usually narrowed at the base, rarely covering the fruits, the venation not conspicuously raised; distal flowers subtended by greatly reduced leaves (ca. 8 mm long) and easily seen [distal internodes usually longer than the adjacent leaves] *B. laxiflora*
 - 5b. Outer sepals to 8 mm long, rounded at the base, usually covering the fruits, venation often conspicuous on the outer surface; distal flowers subtended by normal-size or reduced leaves, usually easily visible 6
 - 6a. Outer sepals not developing a lustrous surface, venation only slightly elevated; plants to 40 (–50) cm tall; distal stems glabrous or glandular puberulent *B. bacopoides*
 - 6b. Outer sepals with smooth lustrous surface and conspicuous elevated venation; plants to 70 cm tall; distal stems glabrous [Belize to Nicaragua] *B. lacertosa*
- 7a. Internodes densely villous with hairs to 1.5 mm long; leaves often suborbicular [outer sepals 4–6 mm long, ciliolate; commonly collected in Costa Rica] *B. salzmanii*
- 7b. Internodes glabrous or with thin hairs < 0.5 mm long; leaves broadly to narrowly obovate (rarely suborbicular) 8

- 8a. Bracteoles 2, slender, below the calyx; outer sepals 5–7 mm long; fruits 4–7 mm long; flowers usually 1/node; pedicels to 30 mm long; internodes glabrous *B. monnieri*
- 8b. Bracteoles none; outer sepals 2.5–4 mm long; fruits 2.3–4 mm long; flowers 1–4/node; pedicels to 18 mm long; internodes glabrous or puberulent 9
- 9a. Sepals (4) 5, unequal and united only at the base; leaves usually cuneate or rounded at the base, sessile; widespread *B. repens*
- 9b. Sepals 4, subequal and united in the lower half; leaves cuneate with a narrowed petiole-like base; rarely collected *B. egenesis*

Bacopa axillaris (Benth.) Standl., J. Wash. Acad. Sci. 15: 460. 1925. *Herpestis axillaris* Benth. in DC., Prodr. 10: 396. 1846. *Monniera axillaris* (Benth.) O. Kuntze, Rev. Gen. Pl. 463. 1891. *Caconapea axillaris* (Benth.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 152. 1920. Figure 1.

Erect **herbs** 10–30 cm tall, aquatic or paludal, rooting mostly at the base, leafy stems 1.3–4 mm diam., spongy, villous with thin multicellular hairs to 1.3 mm long. **Leaves** opposite, sessile with opposing leaves slightly united at the base and forming a line or ridge across the stem (clasping the stem); **leaf blades** 1.2–4.8 cm long, 2–12 mm wide, oblanceolate to narrowly obovate or narrowly elliptic-oblong, apex bluntly obtuse to acute, distal $\frac{2}{3}$ of the margin serrate, teeth 0.2–0.5 mm high, 1–2.3 mm wide, base gradually narrowed and cuneate, drying yellowish brown or olive green, glabrous, conspicuously pellucid punctate beneath, venation pinnate. **Inflorescences** verticillate, of dense axillary fascicles with 3–12 flowers/node, pedicels 0.2–1.5 mm long, expanded at the apex and with 2 small (0.4–0.7 mm) slender bracteoles. **Flowers** glabrous externally, outer sepals 3–4 mm long, 1.5–3 mm wide, ovate with rounded to obtuse apex, palmately veined, punctate, glabrous or ciliate; **corolla** 3–4 mm long, white, slightly exerted, the upper lip 1-lobed; stamens 4, inserted in the upper half of the tube; ovary ca. 1 mm long, style 1.5–2 mm long. **Fruits** 2–3 mm long, ca. 1.4 mm diam., very narrowly ovoid or conical, 4-valved; seeds 0.5–0.6 mm long, 0.2–0.3 mm wide, oblong or somewhat curved, brown, reticulate with parallel longitudinal ridges.

Plants of swamps and the muddy edges of standing water in seasonally deciduous and evergreen forest areas, 0–500 m elevation (to 1500 m in Guatemala). Rarely found north of Panama, the species has been collected near Bagaces and along the Río Grande de Tárcoles in Costa Rica; it flowers in September. The species ranges from Guatemala to Colombia.

Bacopa axillaris is recognized by the pubescent stems, sessile oblanceolate serrate leaves, verticillate flower clusters with small subsessile flowers, and wet habitat. The outer sepals are often flat, translucent, and conspicuously punctate.

Bacopa bacopoides (Benth.) Pulle, Enum. Pl. Surinam. 415. 1906. *Herpestis bacopoides* Benth. in DC., Prodr. 10: 399. 1846. *B. bracteolata* Pennell ex Standl., Contrib. U.S. Natl. Herb. 27: 336. 1927.

Erect **herbs** to 50 cm tall, aquatic or paludal, leafy stems 1.4–4.5 mm diam., glabrous, terete or slightly 4-angled, with minute sessile glands, node lacking interpetiolar lines. **Leaves** sessile, clasping the stem, opposing leaves not united at the base; **leaf blades** 1.5–3.8 cm long, 2.5–7 mm wide, linear-oblanceolate to linear-oblong or ovate-elliptic, gradually narrowed in the lower half but slightly expanded and subauriculate at the base, apex acute, margin serrate with short (0.2–0.3 mm) broad (1–3 mm) teeth, drying dark brown, glabrous, minutely punctate, venation pinnate, obscure. **Inflorescences** of 1–2 axillary flowers (2–4 flowers/node), pedicels 2–7 mm long, 0.2–0.3 mm diam., minutely papillate-puberulent with whitish hairs, slightly expanded at the apex, paired bracteoles 1–2 mm long or absent, linear. **Flowers** glabrous externally or the outer sepals sometimes puberulent, outer 3 sepals 4–8 mm long, 3–5 mm wide, broadly ovate, rounded but obtuse at the base, with raised venation; **corolla** 4–7 mm long, white, stamens 4, inserted near the middle of the corolla tube, anthers ca. 0.6 mm long; ovary glabrous, style ca. 2 mm long. **Fruits** ca. 3 mm long, globose, enclosed within the enlarged (to 15 mm) wing-like sepals.

Partly aquatic plants of marshes and wet areas at low elevations. The species has not been collected in Costa Rica but is common in central Panama and flowers in December–January in Nicaragua. This species ranges from Guatemala to Brazil.

Bacopa bacopoides is recognized by its erect habit, sessile narrow serrate leaves, one or two pedicellate flowers in leaf axils, large rounded outer sepals enclosing the fruits, and wet habitat.

Bacopa egensis (Poepp.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 98: 96. 1946. *Hydranthelium egense* Poepp. in Poepp. & Endl., Nov. Gen. Sp. Pl. 3: 75, tab. 287. 1845.

Aquatic or terrestrial **herbs**, floating or prostrate on wet soil, with short erect flowering stems, rooting at proximal nodes, leafy stems terete, puberulent on the upper surfaces. **Leaves** opposite, larger in aquatic plants, petioles not clearly distinguished from the cuneate base; **leaf blades** 7–23 mm long, 3–14 mm wide, obovate to spatulate, rhombic or suborbicular, apex obtuse to rounded, margin serrate distally, base cuneate from the middle of the blade, puberulent beneath, venation palmate with 5–7 1° veins. **Inflorescences** of solitary axillary flowers (usually 2/node), pedicels 3–6 mm long, slender, glabrous or puberulent, bracteoles absent. **Flowers** with 4-parted calyx 2–4 mm long, lobes united below the middle, subequal, obtuse, subglabrous or the outer surface minutely puberulent; **corolla** 3–5 mm long, funnel-form, white, with 3 unequal lobes rounded distally; fertile stamens 3; ovary with many ovules, stigma bilobed. **Fruits** 3–4 mm long, ovoid, bivalved with membranaceous walls; seeds many, cylindrical-curved, rugulose.

Rarely collected plants of standing water and wet depressions in southern Nicaragua and north-eastern Costa Rica, 0–200 m elevation. Flowering and fruiting in September. The species is also found in Colombia and Brazil.

Bacopa egensis is recognized by its unusual palmately veined leaves with cuneate or attenuate base, flowers with four equal sepals, three-lobed white corollas, and curved cylindrical seeds. The terrestrial plants of this species have smaller leaves with more puberulence than their aquatic conspecifics. We have not seen Costa Rican material and follow the report in *Flora of Nicaragua*.

Bacopa lacertosa Standley is found along the Caribbean coast, from Belize to Nicaragua. It has erect stems to 70 cm tall, lanceolate leaves to 70 × 15 mm, axillary flowers on short pedicels, and broadly ovate outer sepals (to 8 mm long) with a parchment-like texture and lustrous surface on which the venation is conspicuously elevated. Sutton and Hampshire (*Flora of Nicaragua*, 1995) suggested that this species may be conspecific

with the African *B. decumbens* (Fernald) F. N. Williams.

Bacopa laxiflora (Benth.) Wettst. ex Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 180. 1897. *Herpestis laxiflora* Benth. in DC., Prodr. 10: 396. 1846. *H. auriculata* Robinson, Proc. Am. Acad. Arts 26: 172. 1891. *B. auriculata* (Robinson) Greenman, Publ. Field Mus. Nat. Hist. Bot. Ser. 2: 262. 1907. *Caconapea auriculata* (Robinson) Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 150. 1920. *Mella laxiflora* (Benth.) Pennell, Notul. Nat. Acad. Nat. Sci. Philadelphia 46: 1. 1940.

Erect **herbs** 10–40 cm high, aquatic or paludal, rooting only at the base, main stem simple or with few lateral branches, leafy stems 0.5–3 mm diam., glabrous, 4-angled with longitudinal ridges. **Leaves** sessile, smaller and bract-like at distal flowering nodes, often appearing perfoliate but the opposing leaves not united across the stem; **leaf blades** 6–30 mm long, 2–10 mm wide, lanceolate to lanceolate-oblong or ovate-lanceolate, apex acute, margin serrate, teeth ca. 0.3 mm high and 1–2 mm wide, base rounded to auriculate, drying grayish green, glabrous and punctate, venation pinnate. **Inflorescences** of solitary axillary flowers (1–2/node) or racemose and terminal (resembling panicles in some collections), pedicels 3–8 mm long, minutely papillate puberulent, ebracteolate at base of calyx or with 2 slender bracteoles 1–1.5 mm long. **Flowers** glabrous, outer sepals 3–5 mm long, 1–3.3 mm wide, ovate, usually narrowed at the base, acute, palmately veined, inner sepals linear; **corolla** 7–10 mm long, lilac to purple, bilabiate, tube ca. 5 × 1.7 mm, lobes 2–3 mm long; stamens 4, inserted on the upper half of the tube, anthers 0.5 mm long; style 2.5 mm long. **Fruits** 2.5–4 mm long, subglobose, surface slightly reticulate with minute pits; seeds ca. 0.4 × 0.2 mm, oblong with 1 or 2 truncated ends, longitudinally ridged/reticulate, brown.

Plants of wet sites and shallow standing water, in lowland deciduous and evergreen formations, 0–300 m. The species has been collected near La Cruz, Guanacaste Province; it flowers in December–January. The species ranges from Mexico to Brazil but is rarely collected in Central America.

Bacopa laxiflora is recognized by its short erect habit, wet habitat, sessile serrate leaves appearing to clasp the stem, solitary axillary flowers forming distal racemes, and globose or ovoid fruits.

Stems and leaves are usually glabrous, but the pedicels are minutely papillate puberulent.

Bacopa monnieri (L.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 98: 94. 1946. *Lysimachia monnieri* L., Sp. Pl. Cent. 2: tab. 9. 1756. Figure 1.

Prostrate to procumbent **herbs** to 30 cm tall, rooting from the lower nodes, leafy stems 0.7–2.5 mm diam., glabrous, nodes marked by interpetiolar lines. **Leaves** slightly succulent, subsessile or with poorly defined petioles 0.5–2 mm long, clasping the stem at the base; **leaf blades** 3–18 mm long, 1.5–7 mm wide, obovate to oblong-obovate, oblanceolate, or spatulate, apex rounded, margin entire, base gradually narrowed and cuneate, drying yellowish green, glabrous, often punctate, venation pinnate but obscure (sometimes appearing tripliveined). **Inflorescences** of solitary axillary flowers, usually with only 1 flower/node, pedicels 7–30 mm long, 0.3–0.6 mm diam., glabrous, bracteoles 2, opposite, 1.5–3 mm long, 0.4–0.7 mm wide, near the apex of the pedicel and resembling the larger sepals in texture. **Flowers** glabrous, the 2 outer sepals 5–7 mm long, 2–3 mm wide, 3 inner sepals narrower, acute; **corolla** 6–10 mm long, white to lavender, blue or pale purple, lobes rotate and essentially regular, ca. 2 cm wide, tube 3–5 mm long; stamens 4, filaments arising near the apex of the tube, glabrous, anthers ca. 1.5 mm long; ovary ca. 4 mm long, ovate-oblong, style ca. 4 mm long, stigma flattened, ca. 0.8 mm wide. **Fruits** 4–7 mm long, ovoid, enclosed within the persisting sepals; seeds ca. 0.5 mm long, reddish brown, longitudinally reticulate.

Plants of open sunny sites in marshes, sandy stream edges, and standing water, often creeping on wet mud and tolerant of some salinity, 0–1000 m elevation. The species has rarely been collected in Costa Rica, where it is usually found near the coasts. It probably flowers throughout the year. We have seen a single sterile collection (*Crow 9465* INBIO) from 820 m in Alajuela. The species ranges from the southeastern United States to Argentina.

Bacopa monnieri is recognized by its small entire obovate or spatulate leaves, glabrous parts, narrow bracteoles beneath the sepals, somewhat larger flowers, and ability to survive in slightly salty water. The species has been called *verdolaga* in Nicaragua.

Bacopa monnierioides (Cham.) Robinson, Proc. Am. Acad. Arts 44: 614. 1909. *Ranaria monnierioides* Cham., Linnaea 8: 31. 1833. *Herpessis ranaria* Benth. in J. D. Hook., Companion Bot. Mag. 2: 57. 1836, based on *R. monnierioides* Cham. *B. ranaria* (Benth.) Chod. & Hassl., Bull. Herb. Boissier ser. 2, 4: 288. 1904. *Caconapea parviflora* Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 152. 1920. *B. parviflora* (Pennell) Pennell ex Standl., Contrib. U.S. Natl. Herb. 27: 336. 1928. *B. parviflora* (Pennell) Standl. ex L. O. Williams, Fieldiana Bot. 34: 118. 1972.

Erect **herbs** to 40 cm tall, aquatic or in wet soil, with much distal branching, rooting mostly at the base, leafy stems 0.5–2.5 mm diam., minutely puberulent with slender crooked hairs 0.1–0.4 mm long on upper surfaces. **Leaves** sessile, opposing leaves not united across the stem but sometimes producing a line across the stem, distal leaves conspicuously smaller than leaves of the main stem; **leaf blades** 8–30 mm long, 2–7 mm wide, oblong-lanceolate to narrowly oblong, apex obtuse, margin subentire or obscurely dentate with teeth 1–2 mm wide, drying yellowish brown or dark grayish, glabrous, glandular punctate on both surfaces, venation subpalmate or tripliveined. **Inflorescences** mostly fasciculate, of (1)2–4 axillary flowers, 2–8 flowers/node, pedicels ca. 0.5 mm long, bracteoles minute (0.3 mm) at apex of pedicel. **Flowers** glabrous, outer sepals 1–2 mm long, 0.5–1 mm wide, narrowly ovate-oblong, with an unusual glandular-pitted surface; **corolla** 1.5–2.5 mm long, tubular, white or bluish white, upper lobe entire, lower lip 3-lobed; stamens 4, inserted near the apex of the tube; ovary glabrous. **Fruits** ca. 1.5 mm long, smooth, enclosed within the stiff persisting sepals (to 2.5 mm long); seeds 0.6–0.7 mm long, 0.2–0.3 mm thick, oblong-ellipsoid, longitudinally ridged, reddish brown.

Plants of inundated areas, the margins of water bodies, and wet savannas, 0–1500 m in Central America. In Costa Rica, this species has been collected only in lowland Guanacaste. The species ranges from Guatemala to Paraguay.

Bacopa monnierioides is recognized by its erect branching habit, sessile lanceolate-oblong leaves with subserrate margins, small fasciculate flowers, and smooth fruit. The glandular pit at the base of the outer sepal is unusual but difficult to see. Compare *B. axillaris* and *B. sessiliflora*.

Bacopa repens (Sw.) Wettst. in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 76. 1895. *Gratiola repens* Sw., Prodr. 14. 1788. *Herpestis repens* (Sw.) Schldl. & Cham., Linnæa 5: 107. 1830. *Macuillamia limosa* Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 158. 1920. *Bacopa limosa* (Pennell) Standl., Contrib. U.S. Natl. Herb. 27: 336. 1928. *M. repens* (Sw.) Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 60. 1935. *B. curtipes* Standl. & L. O. Williams. Ceiba 3: 129. 1952. Figure 1.

Herbs, aquatic or terrestrial, floating to prostrate or repent, to 40 cm long, rooting from lower nodes, stems 0.4–3 mm diam., glabrous or with short (0.1–0.3 mm) thin hairs distally. **Leaves** sessile, bases of opposing leaves partly united and obscuring the node; **leaf blades** 6–20(–30) mm long, 3–15(–20) mm wide, obovate to obovate-oblong or suborbicular, apex rounded or obtuse, margin entire, base cuneate, drying yellowish green to dark green or blackish, glabrous except near the base, venation palmate with 3–11 major veins. **Inflorescences** of axillary flowers, 2–4 flowers/node, pedicels 6–18 mm long, 0.2–0.3 mm diam., glabrous or minutely puberulent, bracteoles absent or minute. **Flowers** with 4 or 5 sepals, outer sepals 2.5–4 mm long, 0.7–1.5 mm wide, narrowly oblong, rounded to obtuse at the apex, margin often ciliolate, inner sepals narrower; **corolla** 3–4 mm long, white or pale violet, campanulate and regular or nearly so, throat sometimes marked with yellow, 2-lipped, the upper lip 2-lobed; stamens 4, filaments inserted near the apex of the tube, anthers ca. 0.7 mm long; ovary ca. 1.3 mm long, style 1–3 mm long, slender, stigma capitate, slightly 2-lobed. **Fruits** 2.3–4 mm long, ca. 2 mm diam., glabrous, enclosed within the persisting (3–4 mm long) sepals; seeds ca. 0.4 mm long, oblong, dull whitish to brown, surface reticulate.

Aquatic plants of lake edges and marshes, in both evergreen and deciduous forest areas, 0–1000 m elevation. Rarely collected in Costa Rica, this species is found in the Caribbean lowlands and on the Pacific coast in seasonal ponds at Bagaces and Palo Verde National Park. Flowering in August–October. The species ranges from southern Mexico and the West Indies to Argentina.

Bacopa repens is recognized by its aquatic habitat, glabrous or sparsely puberulent stems, obovate sessile leaves slightly united (across the stem) at the base, and small flowers. The distal leaves and stems are often floating and can become a floating mat. This species may be vege-

tatively very similar to *B. monnieri*, but that species has larger flowers and fruits and lacks bracteoles. Compare *B. salzmännii*, which occurs in similar habitats but has villous stems, larger flowers, and separate leaf bases.

Two collections from water 1.5 m deep at Palo Verde National Park (*G. Crow* 5977 & 60603) are provisionally placed here. These collections have larger (20–40 mm) leaves, longer fruits (3–5 mm), and linear-oblong seeds to 0.7 mm long. They conform to the description of *B. valerii* Standl. & L. O. Williams (Ceiba 1: 163, 1950) based on material from 20 m elevation in western Honduras. Although quite distinctive, it seems likely that all these plants represent no more than an unusually robust form of *B. repens*.

Bacopa salzmännii (Benth.) Wettst. ex Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 176, 181. 1897. *Scrophularia procumbens* Vell., Fl. flumin. Ic. 6, tab. 85. 1827, non *B. procumbens* (Miller) Greenman. *Herpestis salzmännii* Benth. in J. D. Hook., Companion Bot. Mag. 2: 58. 1836. *B. salzmännii* (Benth.) Chod. & Hassl. Bull. Herb. Boissier Ser 2.4: 290. 1904. *Monocardia humilis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 157. 1920. *M. violacea* Pennell, loc. cit. 156. 1920. *B. humilis* (Pennell) Standl., J. Wash. Acad. Sci. 15: 460. 1925. *B. violacea* (Pennell) Standl., loc. cit. 460. 1925. *Herpestis ciliata* Pennell, Notul. Nat. Acad. Sci. Philadelphia 46: 2. 1940. Figure 1.

Herbs, aquatic or terrestrial, prostrate or decumbent, sometimes floating or forming mats, rooting from lower nodes, stems succulent, 1–2 mm diam., densely hirsute with thin multicellular hairs 0.7–1.5 mm long. **Leaves** sessile and decussate, opposing leaves not united at the base, often subtended by a tuft of hairs; **leaf blades** 6–20 mm long, 5–18 mm wide, ovate to broadly ovate-elliptic or ovate-orbicular, apex rounded or bluntly obtuse, sometimes slightly notched, margin entire, base rounded and truncate to subcordate or auriculate, drying greenish to yellowish, glabrous or hirsute near the base beneath, venation palmate with 3–7 poorly defined primary veins. **Inflorescences** of solitary axillary flowers, 1–2/node, pedicels 8–23 mm long, 0.2–0.4 mm diam., hirsutulous with slender hairs 0.2–0.5 mm long, ebracteolate (but the outer sepals resembling bracts). **Flowers** with strongly unequal sepals, outer 3 sepals 4–6 mm long, 2.5–5 mm wide, ovate with truncated or subcordate bases and resembling the leaves, ciliolate along the margin, inner sepals

narrowly triangular; **corolla** 6–9 mm long, pale blue to lavender or violet (white), slightly exerted beyond the sepals, 4-lobed with the upper lobe emarginate; stamens 4, included, filaments 1–2 mm long, glabrous, larger anthers 1.2–1.5 mm long; ovary ca. 1 mm long, narrowly ovoid, glabrous, style 2–5 mm long, stigma 0.3 mm wide. **Fruits** ca. 3 mm long and 1 mm wide, narrowly ovoid-oblong; seeds many, small, reddish brown, reticulate.

Plants of shallow water and moist open sunny sites at the edges of water in both evergreen and deciduous forest areas, 40–1700 m elevation. This is a common species of marshes, swamps, and wet depressions, growing both as a partly submerged aquatic, prostrate and mat-forming on wet mud, or erect among other wetland plants, flowering throughout the year. This species ranges from Mexico and the West Indies to southern Brazil.

Bacopa salzmannii is the most commonly collected species of *Bacopa* in Costa Rica. It is recognized by its often aquatic or repent habit in wet sites, the villous stems, sessile rounded leaves, and leaf-like (bract-like) outer sepals. The rounded bases of the leaf blades may obscure the stem but they are not joined (interpitiolar, cf. *B. repens*) nor are they decurrent on the stem.

Bacopa sessiliflora (Benth.) Pulle, Enum. Pl. Surinam 415. 1906. *Herpestis sessiliflora* Benth. in J. D. Hook., Companion Bot. Mag. 2: 58. 1836. *B. sessiliflora* (Benth.) Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 176, 181. 1897, incomplete combination fide D'Arcy 1979. *Caconapea conferta* Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 153. 1920. *C. sessiliflora* (Benth.) Pennell, loc. cit. 75: 11. 1923.

Erect **herbs** to 40 cm tall, with short lateral branches, rooting only at the base, leafy stems 0.8–3 mm diam., glabrous, with 2 opposite longitudinal ridges. **Leaves** sessile, separate at the base and not forming an interpitiolar line, decurrent on the stem, distal leaves smaller (5 mm) and bract-like; **leaf blades** 10–35 mm long, 2–5 mm wide, oblanceolate to linear-oblanceolate or narrowly elliptic-oblanceolate, apex acute, distal half of the margin with prominent teeth ca. 0.5 mm high, 1–2 mm long, cuneate to the base, drying yellowish brown, glabrous, punctate on both surfaces, venation pinnate. **Inflorescences** fasciculate in distal spiciform arrangements or 1–4 flowers in leaf axils, distal spikes 1–3 cm long, ca. 1 cm diam., flowers sessile or subsessile on pedicels less than 1.5 mm long, bracteoles 1–2 mm long

at apex of pedicel or absent. **Flowers** glabrous externally, calyx united at base, outer calyx lobes 3–3.5 mm long, 1.3–2 mm wide, ovate, thin with 3 prominent parallel veins; **corolla** 3–4 mm long, tubular-campanulate, exerted, bluish or white, lobes ca. 0.5 mm long; stamens 4, attached near middle of tube; ovary ca. 1.5 mm long, style ca. 1 mm long. **Fruits** 3–4 mm long, 1.5–2 mm diam., narrowly ovoid, surface with minute (0.1 mm) capitate hairs; seeds ca. 0.3 × 0.2 mm, rectangular with truncated ends, brown, longitudinally reticulate/ridged.

Rarely collected plants of open sunny sites in wet marshes and depressions. The plants are tolerant of brackish water and can be found near the seashore. The species has not been collected in Costa Rica but is known from Bluefields, Nicaragua, and is found in central Panama. The species ranges from Guatemala and Belize to Ecuador and the West Indies.

Bacopa sessiliflora is distinguished by its erect habit, general lack of pubescence, sessile oblanceolate leaves serrulate along their distal margins, and sessile flowers often in axillary fascicles that may be arranged in terminal spike-like inflorescences. Compare *B. monnieroides*.

Benjaminia Martius

REFERENCE—L. B. Smith & J. M. Pires, An evaluation of *Benjaminia* Martius ex Benjamin. J. Wash. Acad. Sci. 46: 86. 1956.

Herbs, aquatic and submerged, rooting at lower nodes, glabrous or puberulent, glandular punctate on vegetative parts. **Leaves** verticillate, united at the base, petiole, the blades pinnatifid with slender linear segments. **Inflorescences** of solitary axillary flowers, bracts absent, pedicels elongating slightly in fruit, bracteoles absent at the base of the calyx. **Flowers** with calyx lobes united near the base, calyx lobes (sepals) 5 and subequal, narrow, valvate in bud; **corolla** tubular and 2-lipped, upper lip slightly 2-lipped, lower lip 3-lobed; stamens 4, of 2 unequal pairs, included, anthers equal, thecae similar; ovary subtended by a ring of filaments, 2-locular, ovules many, style simple, stigma flat and slightly curved. **Fruits** thin-walled capsules, loculicidal, surface smooth; seeds many, oblong, surface longitudinally reticulate.

A monotypic genus of unusual aquatic plants, this taxon is closely related to *Bacopa* but differs in having nearly equal sepals, unusual pinnatifid leaves, and ovary subtended by staminodial fila-

ments (present in some *Bacopa* species). This genus has been confused with the Old World *Limnophila*, but *Benjaminia* is distinct because of its estipitate anther-thecae and its two-lobed stigma. Also, *Limnophila* species usually have emergent leaves that are broad and dentate, whereas emergent leaves are never found in *Benjaminia*. For a short discussion of the complex nomenclature of the genus, see D'Arcy (1979, p. 194).

Benjaminia reflexa (Benth.) D'Arcy, Ann. Missouri Bot. Gard. 66: 194. 1979. *Herpestis reflexa* Benth. in DC., Prodr. 10: 399. 1846. *Beutriculariaeformis* Mart., Fl. Bras. 10: 256. 1847. *Quinquelobulus utriculariaeoides* Benj., Linnæa 20: 316. 1847. *Monnierea reflexa* (Benth.) Kuntze, Rev. Gen. Pl. 2: 463. 1891. *Bacopa reflexa* (Benth.) Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 176. 1897. *Naiadothrix longipes* Pennell, Mem. Torrey Bot. Club 16: 105. 1920. *Bacopa naias* Standl., Field Mus. Bot. Ser. 11: 141. 1932. *Limnophila costaricensis* Suesseng., Bot. Jahrb. Syst. 72: 284. 1942. *L. costaricensis* forma *aquatica* Suesseng., loc. cit. *L. costaricensis* forma *semiterrestris* Suesseng., loc. cit. Figure 1.

Submerged **herbs**, only the flowers and fruits extending above the water surface, branched, rooting at lower nodes, internodes 2–60 mm long, 0.5–2 mm diam., glabrous or minutely and sparsely puberulent, vegetative parts glandular punctate. **Leaves** in verticels of 6 or 8/node (rarely 2 or 4), glabrous or sparsely puberulent, petioles 2–6 mm long (to the first pinna), 0.2–0.4 mm wide; **leaf blades** 4–35 mm long, 5–25 mm wide, with slender filiform pinnate lobes, lobes 4–15/size and in a single plane, central rachis 0.2–0.4 mm wide, lobes 0.05–0.15 mm wide, often with small (0.1–0.2 mm) punctate glands. **Inflorescences** of solitary axillary flowers, 1 flower/node, pedicels 5–9(–18) mm long, 0.2–0.4 mm diam., glabrous or sparsely and minutely puberulent. **Flowers** with sepals 2–4 mm long, 0.4–0.7 mm wide, linear-lanceolate to linear-oblong, apex usually slightly rounded; **corolla** 4–6 mm long, bluish white or purple, yellowish within the throat; anthers versatile and similar; ovary ca. 2 × 1 mm, narrowly ovoid, style ca. 1 mm long, slender. **Fruits** 2–3 mm long, narrowly ovoid, smooth, with a persisting style ca. 1 mm long; seeds ca. 0.6 mm long, oblong-fusiform, reticulate.

Submerged aquatic plants of shallow ponds and lakes, 0–800 m elevation. Only three collections from Costa Rica have been seen, all from the

General Valley (near Buenos Aires and between San Isidro and Rivas), flowering and fruiting in November (*Crow* 6176 & 6239), December (Nicaragua), and February (*Kupper* 597). The species (in a wide sense) ranges from Mexico and Cuba to Brazil.

Benjaminia reflexa is an unusual aquatic plant distinguished by being almost entirely submerged, having whorls of feather-like leaves with slender pinnate lobes, solitary little flowers with five nearly equal narrow sepals, and sympetalous two lipped corollas. The flowers and fruits are borne above the water surface on stiff pedicels. The leaves can also be interpreted as being opposite, with each leaf having three or four primary axes and each of these having deeply divided pinnatifid divisions. These plants resemble the submerged portions of species of *Cabomba* (Nymphaeaceae) as well as aquatic *Utricularia* species (Lentibulariaceae). The only similar Neotropical species of Scrophulariaceae is *Bacopa myriophylloides* (Benth.) Pennell, which has palmately dissected leaves and differing flowers. This species was treated as *Bacopa naias* in the *Flora of Guatemala*. Suessenguth's *Limnophila costaricensis* lacks a species description but has Latin descriptions of two forms, all based on a single collection number (*Kupper* 597, fragments at F).

Buchnera Linnaeus

REFERENCE—D. Philcox, Revision of the New World species of *Buchnera* L. Kew Bull. 18: 275–316. 1965.

Herbs, annual (in ours) or perennial, hemiparasitic, erect, simple or branched, hairs with a broad base and stiff straight tip, often scabrous, drying dark. **Leaves** opposite or subopposite, sometimes alternate distally, sessile to short-petiolate, leaf blades narrow, dentate or entire, margins often revolute, usually scabrous, venation pinnate or palmate, with 1 or 3 (5) major veins. **Inflorescences** terminal compact or lax spikes, flowers sessile or subsessile, subtended by a bract, with 2 slender lateral bracteoles beneath the calyx. **Flowers** with a tubular calyx, slightly enlarging in fruit, with 5 or 10 prominent longitudinal veins, lobes 4 or 5, shorter than the tube, acute; **corolla** radially symmetric and usually salverform, tube longer than the calyx, cylindrical and straight or slightly curved, blue to white or purple, glabrous (in ours) or puberulent externally, lobes 5 and

subequal, rotate-spreading, shorter than the tube, apex of the tube often with moniliform hairs; stamens 4, of 2 unequal pairs, inserted in the proximal half of the tube, sessile or with short filaments, anthers ovoid, versatile, 1-theccous; ovary ellipsoid to ovoid, 2-locular with many ovules, style slender and included, stigma clavate. **Fruits** dry capsules partly enclosed by the persisting calyx, splitting loculicidal into 2 equal parts; seeds many, oblong or ellipsoid, curved or angled, longitudinally reticulate.

A genus of ca. 100 species in tropical and tem-

perate climates throughout the world. Most of the species are found in the Old World tropics; there are about 16 species in the New World. The genus is distinguished by its slender few-branched habit, stiff, narrow, usually scabrous leaves, spicate inflorescences, tubular calyx, and one-theccous anthers, all parts drying dark or black. All species are believed to be hemiparasites, attaching by haustoria to the roots of the host plants. The genus is placed in the tribe Buchnerae, along with many Old World genera. Its closest Neotropical relatives are *Alectra* and *Escobedia*.

Key to the Species of *Buchnera*

- 1a. Stems hispid-scabrid, rough to the touch; larger leaves with prominent teeth; calyx pubescent, becoming slightly thickened in fruit, but the areas between the longitudinal veins usually remaining flat and the minor venation not visible *B. pusilla*
- 1b. Stems usually smooth to the touch at distal internodes; larger distal leaves entire and linear; calyx glabrous, becoming conspicuously thickened and with raised minor venation between the longitudinal veins in fruiting stages *B. weberbaueri*

Buchnera pusilla Kunth in H.B.K., Nov. Gen. Sp. 2: ed. quarto 340. 1818. *B. tinctoria* Bertol., Fl. Guatemala 26. 1840. *B. major* Polak., Linnaea 41: 588. 1877. *B. mexicana* Hemsl., Biol. Centr. Am. Bot. 2: 457. 1881. Figure 4.

Stiff erect **herbs** (6-)10-70(-150) cm tall, annual, unbranched or with 2-7 distal branches, drying dark, stems 0.4-3 mm diam., terete, hispid with stiff whitish hairs 0.3-1.3 mm long. **Leaves** opposite or subopposite, sessile or with poorly differentiated petioles to 8 mm long; **leaf blades** 15-50 mm long, 1-8 mm wide, linear to linear-oblong or linear-oblancheolate (oblong near the base), apex acute, margin with 1-5 prominent teeth (0.2-1 mm) or entire, gradually narrowed to the cuneate base, subcoriaceous, with scattered short scabrid hairs above, larger (0.2-0.5 mm) stiff hairs along the margin and veins beneath, with 1 or 3 major veins. **Inflorescences** 3-15 cm long, bracts 4-9 mm long, ovate to lanceolate, pedicels 0-1 mm long, with 2 shorter linear bracteoles beneath the calyx, bracts and bracteoles scabrid and ciliate. **Flowers** with calyx 4-5 mm long, enlarging (to 8 mm) and becoming more scabrid in fruit, with 10 longitudinal veins, hispid only along the veins, lobes 1-2.5 mm long, equal or unequal, acute; **corolla** 8-14 mm long, salverform, white to purplish white or lilac, tube 0.4-0.8 mm diam., lobes 1-5 mm long, obovate with narrowed base and broadly rounded apex; stamens

inserted near the middle of the tube. **Fruits** 4-6 mm long, ca. 2 mm wide, oblong, smooth, partly enclosed in the scabrid calyx; seeds 0.4-0.5 mm long, oblong or curved.

Plants of open sunny sites in fields and savannas in deciduous and evergreen forest areas of the Pacific slope and central highlands, 10-1700 m elevation. Flowering and fruiting from October to early March. The species ranges from Mexico to Ecuador and Brazil.

Buchnera pusilla is distinguished by its short, stiff, erect (usually few-branched) habit, hispid to scabrous vestiture, spicate inflorescences, and salverform white to pinkish corollas, all parts turning dark when dried. This is a frequently collected species in Central America. We have included *Herrera 801* within our concept of this species, which has been identified as *B. longifolia* Kunth by Wilcox (1965, see above). *Buchnera pusilla* and *B. longifolia* form a variable species complex, widely distributed in the lowland Neotropics. They are distinguished by the amount and type of pubescence on the calyx, but that character can vary with the age of the flower, the fruits becoming more scabrid as they mature. See the illustration in *Flora of Guatemala* (Standley & Williams, 1973, p. 337).

Buchnera weberbaueri Diels, Bot. Jahrb. Syst. 37: 430. 1906. *B. leiantha* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 105. 1940.

Stiff erect **herbs** 30–70 cm tall, annual, usually without lateral branches, leafy stems 1–2.5 mm diam., glabrous or with minute (0.1–0.2 mm) scabrid hairs in longitudinal files or at lower internodes, usually smooth to the touch. **Leaves** opposite or subopposite, sessile and slightly clasping the stem, a petiole not differentiated; **leaf blades** 2–7 cm long, 0.5–4 mm wide, linear to linear-lanceolate, apex acute, margins entire (except rarely on basal leaves), base gradually narrowed, drying black or brown, glabrous, with 1 central vein or tripliveined. **Inflorescences** 4–14 cm long, flowers separate or closely congested into a dense spike, abaxial bracts 2–3 mm long, acute, enlarging to 5 × 3 mm in fruit, ciliolate along the margin, pedicels 0–1 mm long. **Flowers** with calyx 5–7 mm long, to 10 mm in fruit, sparsely puberulent with few white hairs, sepal lobes ca. 1.5 mm long, acute, minor venation between the main veins not apparent until fruiting; **corolla** 7–13 mm long, salverform, lilac to pink-purple or white, tube ca. 0.6 mm diam., lobes 1.5–2 mm long, equal. **Fruits** 5–7 mm long, ca. 3 mm diam., surface smooth and glabrous, included within the stiff thickened calyx.

Rarely collected plants of open sunny sites, 200–1300 m elevation. In Costa Rica this species has only been collected in Guanacaste Province, flowering in January and September–October, with old fruit in February. The species has been collected in Belize, in Izabal (Guatemala), and on the Cerro de Espíritu Santo near Naranjo in Costa Rica; it ranges southward to Trinidad and Peru.

Buchnera weberbaueri is recognized by its short, usually unbranched stems, very sparse pubescence, linear entire leaves, and sepals that become indurated and with many elevated veins in fruiting stages. Two rather different specimens are provisionally placed here: *Herrera 801*, with young flowers, and *Williams & Williams 24514*, with old fruits. Standley and Williams (1973) confused *B. weberbaueri* with the larger-flowered *B. palustris* (Aubl.) Spreng., which is found in lowland South America in wet areas. In addition to its larger flowers, *B. palustris* has longer pedicels and narrowly lanceolate bracts and bracteoles.

Calceolaria Linnaeus

REFERENCES—U. Molau, Scrophulariaceae, Part 1. Calceolariae. Fl. Neotropica, Monogr. 47: 1–326. 1988. L. R. Landrum & R. McVaugh, *Calceolaria mexicana* and *C. tripartita* in Mexico. Contrib. Univ. Michigan Herb. 11: 273–309. 1978.

Shrubs, vines or herbs, annual or perennial, usually confined to high-elevation habitats, stems terete, hairs simple. **Leaves** opposite (ternate in some Andean species), sessile or petiolate, leaf blades simple and without prominent lobes or becoming deeply lobed or pinnatifid, margins usually serrate, pinnately veined. **Inflorescences** terminal or axillary, often a compound thyrses of cymes with 3 or 4 flowers or of 1–3 axillary flowers, often subtended by smaller leaves, bracteoles absent at the base of the calyx. **Flowers** small to large, calyx deeply 4-parted, sepal lobes equal or unequal, valvate in bud, usually persisting in fruit; **corolla** strongly bilabiate with the lower lip usually developed into a globose or slipper-like saccate form, the upper lip usually much smaller and arched or hooded and enclosing style and stamens, yellow to red or purple, sometimes spotted or mottled, glabrous on the exterior; stamens 2, attached near the base of the tube, filaments short, anther with 2 contiguous thecae opening by a longitudinal slit, staminodes absent; ovary superior and conical (partly inferior in the temperate subgenera *Cheiloncos* and *Rosula*), somewhat 2-lobed, 2-locular, ovules many, style short and often recurved, stigma simple or capitate. **Fruits** dry capsules, septicidal and loculicidal, the 4 valves opening from the apex; seeds many, small (0.3–1 mm), usually with longitudinal and transverse ridges or minute tubercles.

A pantropical genus of ca. 300 species with a majority of the species found above 1000 m elevation in the Andes. A number of species range into the lowlands of temperate Chile and Argentina. The genus is classified with *Jovellana* and *Porodittia* in the tribe Calceolariae. This tribe exhibits links between southern South America and New Zealand, duplicating the disjunction found in the tribe Veroniceae. Molau (1988) provided a fine treatment of this complex and fascinating group in the Neotropics; his discussions of biology, distribution, speciation, and phylogeny are especially noteworthy. *Calceolaria* is immediately recognizable because of its bright yellow bilabiate corollas with small upper lip and rounded saccate or inflated slipper-like lower lip. The four-parted calyx, only two stamens, and restriction to moist high-elevation habitat (in Central America) are further distinctions. Some South American species have corollas that are somewhat S-shaped in lateral view. A number of hybrids are popular as potted ornamentals, called “slipper-worts” or “slipper flowers.”

Key to the Species of *Calceolaria*

- 1a. Petioles broadly winged to the base and united across the node, the leaves perfoliate [larger blades triangular to sagittate, never pinnatifid; anther cells contiguous, dark brown; uncommon] *C. perfoliata*
- 1b. Petioles not broadly winged to the base, the leaves not perfoliate 2
- 2a. Larger leaves lanceolate, without pinnate lobes or deep sinuses; anther-thecae contiguous, not separated by an expanded connective; stems slightly woody and plants clambering to 2 m high (note that these 2 species are very similar) 3
- 2b. Larger leaves usually with prominent pinnate lobes separated by deep sinuses; anther-thecae separated by the slender expanded connective; stems mostly herbaceous and semisucculent, plants to 1 m high 4
 - 3a. Fruits puberulent; 2° veins of leaves not loop-connected in the distal half of the blade, usually strongly ascending, upper surface of the blade with very short hairs and glands, lower surface often with brown punctations; stems usually puberulent; seeds with prominent longitudinal ridges and smaller transverse ribs; common high-montane plants *C. irazuensis*
 - 3b. Fruits glabrous; 2° veins of leaves usually loop-connected in the distal half of the blade, upper surface lacking very short hairs or glands, lower surface not punctate; stems usually glabrous (rarely with a few hairs at nodes and petioles); seeds with prominent longitudinal ridges but no transverse ribs; rarely collected in Costa Rica *C. microbefaria*
- 4a. Corolla 5–15 mm long, mouth open; fruits 3–7 mm long, oblate; seeds 0.4–0.5 mm long; sinuses of larger leaves rarely reaching the midvein; lower anther-theca fertile *C. mexicana*
- 4b. Corolla 10–20 mm long, mouth closed; fruits 6–9 mm long, ovoid; seeds 0.6–0.8 mm long; sinuses of larger leaves sometimes reaching the midvein; lower anther-theca sterile *C. tripartita*

Calceolaria irazuensis J. D. Smith, Bot. Gaz. 20: 292. 1895. *C. costaricensis* Kränzl., Ann. K. K. Naturhist. Hofmus. 22: 192. 1907. Figure 3.

Subshrubs, erect or scandent, 0.2–1(–2) m tall, leafy stems 1.2–5 mm diam., densely puberulent with slightly viscous hairs 0.05–0.3 mm long, older stems glabrescent. **Leaves** forming a line across the stem at their base, petioles 2–8(–15) mm long, 0.5–1.8 mm diam., puberulent with longer hairs adaxially; **leaf blades** 1.8–9(–12) cm long, 6–35(–45) mm wide, lanceolate to ovate-lanceolate or elliptic-lanceolate, gradually narrowed to the acute apex, margin serrate with teeth 0.3–1 mm high, 2–5 teeth/cm, base acute to obtuse or slightly rounded, asymmetric, drying much paler beneath than above, minutely (0.1–0.2 mm) puberulent above, glabrous between the veins beneath, 2° veins 4–9/side and strongly ascending. **Inflorescences** mostly of 2–4 long-pedunculate cymes subtended by a pair of smaller leaves (bracts) or with 2–4 flowers terminal on the distal leafy node, minutely viscid puberulent, peduncles 1.5–12 cm long, 1–2 mm diam., usually bearing 3 or 4 pedicellate flowers, pedicels 1–4 cm long, 0.4–0.6 mm diam. **Flowers** with calyx 6–9 mm long, calyx lobes 4–9 mm long, broadly ovate-triangular, minutely puberulent along the margin; **corolla**

12–24 mm long, minutely glandular-papillose on the exterior, upper lip 6–8 mm long, lower lip 15–25 mm long, 12–18 mm wide, bright yellow; filaments ca. 1.5 mm long, anthers with divaricate thecae to 3.5 mm wide; style 2–3 mm long, curved. **Fruits** 6–9 mm long, 5–8 mm wide, ovate with truncated base, minutely papillate-puberulent; seeds 0.4–0.7 mm long, 0.2–0.3 mm wide, oblong-ellipsoid, dark brown, with prominent longitudinal ridges and minute transverse ribs (×50).

Plants of evergreen high-montane forest formations, (1800–)2400–3500 m elevation. Flowering and fruiting throughout the year but with most collections made between November and May. The species ranges from Volcán Barva southward to the Chiriquí highlands of Panama.

Calceolaria irazuensis is recognized by its mostly lanceolate leaves, slightly viscid hairs, inflorescences often with long peduncles and/or pedicels, and slipper-shaped yellow flowers. This species is frequently encountered in open sites at higher elevations. Compare the closely similar but rarely collected *C. microbefaria*. Common names are *botón de oro* and *gallitos*.

Calceolaria mexicana Benth., Pl. Hartw. 47. 1840. *C. trachelifolia* Martens & Galeotii, Acad. R. Sci. Bruxelles 12: 16. 1845. *C. urti-*

cina Kränzl., Feddes Repert. Spec. Nov. Regni Veg. 1: 82. 1905. Figure 3.

Annual **herbs**, erect to decumbent, 10–60(–100) cm tall, leafy stems 0.6–3 mm diam., slightly succulent, often reddish in color, sparsely to densely puberulent with simple or viscid gland-tipped hairs 0.3–0.6 mm long. **Leaves** slightly clasping the stem and forming an interpetiolar ridge, petioles 2–40(–160) mm long, 0.4–1.4 mm diam., pubescence similar to that of the stem; **leaf blades** 1–12 cm long, 0.4–8(–13) cm wide, varying from narrowly ovate-triangular in smaller blades to broadly ovate-triangular in outline with 2–4 prominent pinnatifid lobes separated by deep sinuses in larger blades, apex acute, margins strongly dentate-serrate with intermixed larger (2–4 mm) and smaller (0.3–2 mm) teeth, base obtuse to subcordate, drying yellowish green to grayish green, upper surface with slender hairs 0.2–0.4 mm long, lower surface with few thin hairs to 1 mm long on the major veins, 2° veins 6–12/side. **Inflorescences** of solitary axillary flowers (2/ node) or resembling terminal cymes when subtended by reduced bract-like distal leaves, pedicels 4–14 mm long, elongating in fruit, 0.15–0.25 mm diam., minutely puberulent with gland-tipped hairs. **Flowers** with calyx 4–6 mm long, calyx lobes 2–5 mm long, 1–3 mm wide at the base, acute, with glandular hairs at the base; **corolla** 5–15 mm long, 3–10 mm wide, the upper lip 1–3 mm long, lower lip 5–14 mm long, 3–6 mm wide, slipper-shaped, yellow; anthers 2–3.5 mm wide, the 2 small thecae fertile, separated by the longer narrow connective; ovary 2.5 mm diam., papillate-puberulent. **Fruits** 3–7 mm long, 3–6 mm wide, oblate or globose, thin-walled; seeds 0.4–0.5 mm long, ca. 0.3 mm thick, oblong, dark.

Plants of wet sites near streams, moist depressions, and wet cliffsides, 1500–3200 m elevation. Flowering throughout the year, but with most Costa Rican collections made in April–August. This species is the commonest *Calceolaria* in Mexico and Central America; it ranges to Bolivia.

Calceolaria mexicana is recognized by its preference for wet montane habitats, diverse foliage with the large leaves having prominent pinnate lobes, small slipper-shaped yellow corollas, and stamens with two small but functional thecae. This species can be found growing together with the very similar *C. tripartita*, and the two are easily confused. Both species have a strongly developed connective separating the thecae. In *C. mexicana* the corollas are open and the lower lip is

slightly three-lobed. In addition, the larger leaves do not have the deep sinuses of *C. tripartita* leaves.

Calceolaria microbefaria Kränzl., Ann. K. K. Natur. Hofmus. Wien 22: 193. 1907. *C. storkii* Standl., Publ. Field Mus. Nat. Hist. Bot. Ser. 18: 1103. 1938.

Shrubs or subshrubs 0.3–3 m tall, erect or clambering, much branched, stems glabrous or with a few hairs at the nodes. **Leaves** with petioles 3–11 mm long, glabrous or with a few hairs along the adaxial margins; **leaf blades** 4–9(–13) cm long, 1–2.3(–2.8) cm wide, lanceolate to narrowly oblong-lanceolate, apex acute, margin serrate with 5–7 gland-tipped mucronulate teeth/cm, base acute, upper surface glabrous or minutely papillate, lower surface often drying pale grayish or reddish, 2° veins 5–11/side, loop-connected distally. **Inflorescences** 3–12 cm long, usually with 2 or 3 pairs of 4–8 flowered cymes, peduncles 1–5 cm long, bracts often lacking at the base of the cymes, pedicels 0.5–3.4 cm long, glabrous to minutely papillate-puberulent (to tomentose in South America). **Flowers** with sepals 3.3–6 mm long, 2.8–4 mm wide at anthesis, minutely puberulent along the margins; **corolla** 10–20 mm long, bright yellow, the upper lip hooded or flattened and sub-circular, the lower lip projecting or pendant, saccate; anthers 2–3.7 mm wide. **Fruits** 5–9 mm long, 5–9 mm wide, broadly ovoid with truncated base, glabrous; seeds 0.7–0.9 mm long, ca. 0.3 mm thick, with prominent longitudinal ridges, surface smooth.

Plants of subparamo formations near the highest point along the Interamerican Highway in the western part of the Talamanca range, 3100–3500 m elevation. Flowering in March–August; fruiting in August. This species is known from only four collections in Costa Rica (*Barringer et al.* 2913, *Grayum & Affolter* 8190, *Skutch* 5188, and *Stork* 3048, type of *C. storkii*). The species ranges from Venezuela to central Ecuador in the Andes, with a small disjunct population in Costa Rica.

Calceolaria microbefaria is recognized by its lanceolate leaves, generally glabrous vegetative parts and fruits, bright yellow slipper-shaped corollas, and very limited range in our area. Molau (1988) divides this species into three geographically and morphologically distinct subspecies, with the Costa Rican collections placed in subspecies *microbefaria*. In Costa Rica, this species is easily mistaken for the much more common *C. irazuensis*.

sis; the characteristics used in the key to separate the two species usually allow confident identification.

Calceolaria perfoliata L.f., Suppl. 86. 1781. *Fa-gelia perfoliata* (L.f.) Kuntze, Rev. Gen. Pl. 2: 460. 1891. *C. sciadephora* J. D. Smith, Bot. Gaz. 25: 151. 1898. Figure 6.

Herbs or weak-stemmed shrubs 0.5–1.5 m high (to 5 m long), often scandent on other plants, leafy stems 1.5–6 mm diam., often with 4 prominent longitudinal ridges, slightly succulent, with slender crooked multicellular hairs 0.3–1 mm long. **Leaves** sessile and perfoliate, opposing leaves united at the base with lateral tissue to 6 mm wide, leaves subtending the inflorescences not perfoliate, petioles broadly winged and blade like, 0.5–6 cm long, 3–12 mm wide and expanded near the stem; **leaf blades** 2–11 cm long (beyond the blade-like petiole), 2–7 cm wide, narrowly triangular or sagittate, apex acute, margins serrate-dentate with larger (2–4 mm) and smaller (1–2 mm) teeth intermixed, base truncated to the winged petiole-like part, drying yellowish brown, often silvery below (in life), upper surface with short (0.2 mm) scattered hairs, lower surface with thin hairs to 1 mm long, 2° veins 5–7/side. **Inflorescences** with 8–12 (4–24) flowers, borne on axillary peduncles 6–15 cm long, 1–1.5 mm diam., terminated by a pair of asymmetric leaves/bracts 2–5 cm long, pedicels 1.5–5 cm long, densely puberulent. **Flowers** with calyx 8–12 mm long, lobes 6–8 mm long, puberulent, broadly ovate, rounded at base, apex obtuse, enlarging slightly in fruit; **corolla** to 22 mm long, bright yellow, upper lip 4–9 mm long, lower lip 15–20 mm long, 8–18 mm wide, anthers U- or C-shaped, 2–4 mm wide; ovary pubescent, style 3–5 mm long. **Fruits** 5–7 mm long, ca. 5 mm diam., ovoid with truncated base, pubescent; seeds 0.5–0.7 mm long, 0.1–0.2 mm wide.

Infrequently collected plants of evergreen montane forest formations, 2700–3300 m elevation (as low as 1800 m in Chiriquí). Flowering and fruiting appear to be restricted to January–February in Costa Rica. This species ranges from the Cordillera de Talamanca and the Chiriquí highlands to southern Ecuador.

Calceolaria perfoliata is distinguished by its perfoliate leaves with broadly winged petioles and distal narrowly triangular or sagittate blades. The anthers are attached at the center and decurved laterally to produce a rounded C-shaped or horse-

shoe-shaped form. The restricted flowering period may account for the relatively few Costa Rican collections. A related species, *C. trilobata* Hem-sley, is native to Mexico–Guatemala and Venezuela–Bolivia but is not known from southern Central America. That species has a more definitely contracted petiole between the distal blade and the expanded perfoliate base, and the anthers are not horseshoe-shaped.

Calceolaria tripartita R. & P., Fl. Peruv. Prodr. 1: 14, tab. 22. 1798. *C. heterophylla* Wild., Enum. Pl. 1: 29. 1809 (non *C. heterophylla* R. & P.). Figure 3.

Herbs, erect or decumbent, 9–90 cm tall, stems 1–4 mm diam., slightly succulent, puberulent with multicellular, often gland-tipped hairs 0.2–0.7 mm long. **Leaves** simple and serrate to deeply pinnatifid, slightly clasping the stem and forming a ridge across the node, petioles 1–5 cm long, 0.5–1.5 mm wide, glandular puberulent; **leaf blades** 1–16 cm long, 0.3–11 cm wide, ovate-lanceolate in smaller leaves to broadly ovate-triangular, larger blades with deep proximal sinuses separating 1–3 pairs of subopposite lobes, apex acute, margin with larger (3–10 mm) and smaller (0.3–3 mm) teeth, base truncated in larger leaves, drying greenish or brown, upper surface with transparent multicellular hairs to 1 mm long. **Inflorescences** of terminal or axillary flowers, 2–4/node (if small distal leaves are interpreted as bracts, the subtending internodes can be interpreted as peduncles of thyrses-like inflorescences), pedicels 4–45 mm long, 0.2–0.4 mm diam., puberulent with simple or glandular hairs 0.2–0.4 mm long. **Flowers** with calyx 5–7 mm long, lobes ca. 4 mm long, with small glandular hairs; **corolla** 10–20 mm long, bright yellow, upper lip 2–5 mm long, lower lip 10–25 mm long, 6–15 mm wide, slipper-shaped, unlobed; anthers 2–5 mm long, one theca sterile, reduced to a nub, connective slender. **Fruits** 6–9 mm long, ovoid, rounded at the apex; seeds 0.6–0.8 mm long, ca. 0.4 mm diam., reddish brown, with longitudinal ridges.

Plants of wet or moist open sites in evergreen montane forest formations, 1000–3200 m elevation. Flowering throughout the year, but with most collections made between October and December. This species ranges from Mexico to Peru.

Calceolaria tripartita is recognized by its highland habitats, glandular viscid pubescence, larger leaves deeply pinnatisect (almost pinnately compound), yellow slipper-shaped corollas, and un-

usual stamens. This species is similar to *C. mexicana* (q.v.), and the two have often been confused, as in the *Flora of Guatemala*. In addition to the differences used in the key, the pedicels of *C. tripartita* usually have more conspicuous gland-tipped hairs.

Capraria Linnaeus

REFERENCES—T. A. Sprague, A revision of the genus *Capraria*. Kew Bull. 1921: 205–212. 1921. C. Niezgodna & S. Tomb, Systematic palynology of the tribe Leucophylleae (Scrophulariaceae) and selected Myoporaceae. Pollen et Spores 17: 497–516. 1975.

Herbs or subshrubs, annual or perennial, branches usually slender and terete, pubescent or glabrous. **Leaves** alternate, sessile or petiolate, blades usually serrate, glandular punctate (viewed by transmitted light). **Inflorescences** of 1–3 axillary flowers borne on slender pedicels at distal nodes (racemose when distal leaves are reduced and bract-like), bracteoles absent beneath the calyx. **Flowers** radially symmetric, calyx united only near the base, sepals 5, equal or subequal, narrow, valvate in bud; **corolla** funnellform or campanulate, white, purple, or greenish yellow, glabrous externally, tube as long as the lobes or slightly shorter, lobes 5, throat sometimes bearded within; stamens 4 or 5, equal or subequal, included, borne proximally or distally within the tube, filaments glabrous, anthers sagittate, basifixed, versatile, introrse, thecae divergent but basal parts confluent; ovary 2-locular, ovules many, style slender, apically flattened with stigmas on the lateral faces. **Fruits** capsules, ellipsoid to ovoid, glandular-punctate, dehiscent loculicidally and secondarily septicidal, 4-valved, placenta remaining as a conspicuous column with pitted-reticulate surface; seeds many, small, yellow to brown.

Capraria is a genus of five species ranging from the southern United States to Peru; one species is adventive in West Africa. The narrow alternate leaves, flowers that are radially symmetric, and fruit with persisting reticulated column (placenta) make these plants distinctive. The campanulate five-lobed corolla and five stamens are unusual in the Scrophulariaceae, so that the genus has never been satisfactorily classified within the family. Niezgodna and Tomb (reference above) showed that the pollen of *Capraria* is diorate and more closely related to types found in the My-

oporaceae than to the pollen of other Scrophulariaceae.

Capraria biflora L., Sp. Pl. 628. 1753. *C. biflora* var. *pilosa* Griseb., Fl. Brit. W.I. 427. 1861. *C. biflora* form *hirta* Loes., Bull. Herb. Boissier 2, 3: 284. 1903. Figure 7.

Herbs or **subshrubs**, perennial, erect or clambering, 0.5–2 m tall, distal stems usually few-branched, leafy stems 0.7–5 mm diam., densely puberulent to glabrescent with thin erect whitish hairs 0.2–0.7 mm long. **Leaves** alternate, gradually becoming smaller on distal stems, petioles to 8 mm long but usually not clearly differentiated; **leaf blades** 1.5–11 cm long, 6–30 mm wide, elliptic to elliptic-oblongate or oblongate, apex acute and sharp-tipped, distal half of the margin with sharp-pointed teeth 0.5–3 mm high, 1–6 teeth/cm, gradually narrowed to the cuneate base, drying grayish green, both surfaces with thin white hairs 0.1–0.4 mm long, 2° veins 3 or 4/side, strongly ascending. **Inflorescences** of 2 or 3 flowers in distal leaf axils, pedicels 4–12 mm long, ca. 0.2 mm diam., minutely puberulent, not articulated at the base of the calyx. **Flowers** with calyx 4–6 mm long, sepals 1–1.5 mm wide at the base, narrowly triangular to linear, to 7 mm long in fruit, with short (0.3 mm) thin whitish hairs; **corolla** 7–10 mm long, 4–7 mm wide at the mouth, tubular-campanulate, white, lobes 3–5 mm long, 2.5–3.5 mm wide at base, triangular; filaments attached at the base of the tube, 3–4 mm long, anthers ca. 3 mm long. **Fruits** 4–6 mm long, 2.5–4 mm wide, ovoid-ellipsoid and bisulcate, surface smooth, yellowish brown and punctate; seeds 0.3–0.4 mm long, oblong or angular.

Plants of open sunny sites in lowland situations in both the Caribbean (evergreen) and northern Pacific (deciduous) areas of Costa Rica, 0–500 m elevation (to 1000 m in Nicaragua). Flowering and fruiting throughout the year but collected primarily in July–January. The species ranges from Florida, Mexico, and the West Indies to Argentina; it is found on Cocos Island and has become naturalized in West Africa.

Capraria biflora is recognized by its long slender stems, alternate leaves that are smaller distally, oblongate leaf blades serrate in the distal half, flowering nodes with two or three flowers on slender pedicels, and flowers with narrow sepals and radially symmetric campanulate white corolla. The glandular punctations of the leaves can best be seen by transmitted light. This species is

uncommon in Central America. In Panama it is used to make a tea that may be a dangerous depressant in large quantities (D'Arcy, 1979).

Castilleja Mutis ex Linnaeus filius

REFERENCE—N. H. Holmgren, *Castilleja* (Scrophulariaceae) in Costa Rica and Panama. *Brittonia* 30: 182–194. 1978.

Herbs or subshrubs, annual or perennial, erect, branching mostly from the base, hemiparasitic on roots of hosts, drying dark. **Leaves** alternate, cauline, sessile or the petioles poorly differentiated, leaf blades entire to deeply dissected or pinnately lobed. **Inflorescences** terminal spikes or racemes, spikes usually with flowers hidden by colorful bracts, the racemes often with conspicuous flowers arranged along one side (secund), subtending leaves intergrading with bracts, distal bracts often more conspicuous than the flowers, bracteoles absent at the base of the calyx. **Flowers** bilaterally symmetric, calyx tubular with 4 equal or unequal lobes or united into 2 entire lateral lobes, slightly enlarging in fruit; **corolla** bilaterally symmetric and strongly 2-lipped, greenish yellow to brightly colored, tube usually elongate and narrow, upper (adaxial) lip entire with united lobes hooded and forming a beak-like galea, enclosing the anthers, lower lip slightly 3-saccate, with 3 rudimentary

teeth or petaloid lobes; stamens 4, of 2 unequal pairs, attached near or above the middle of the corolla tube, anther sacs (thecae) unequally placed on the connective, the outer longer and attached near the center, the inner theca smaller and borne on the apex of the connective; ovary 2-locular, ovules many, style slender, stigma capitate or slightly 2-lobed. **Fruits** dry capsules, usually asymmetric, ovate to globose, opening loculicidally; seeds many, with a loose reticulate exotesta.

A genus of ca. 200 species, ranging from North America into higher elevation Central America and the Andes, and with a few northern Asian and European species. These plants are easily recognized because of their colorful inflorescences in which bracts, sepals, and petals may all be variously colored and showy. The calyx tube is somewhat gibbous at the base (abaxially) and often with only two large lateral lobes; the narrow, curved corolla has a beaked upper lip that is usually much longer than the lower lip. In many species all parts become blackish on drying. Many species of *Castilleja* have the reputation of being very variable and difficult to distinguish, making the delimitation of some species quite arbitrary. This problem manifests itself in Costa Rica, where *C. irasuensis*, *C. quirosii*, and *C. talaman-censis* form a closely related complex that deserves further study. Our treatment is based on the publication (1978, cited above) and determinations of Noel Holmgren.

Key to the Species of *Castilleja*

- 1a. Calyx 9–12 mm long, corolla 9–12 mm long; flowers sessile and difficult to see within the densely congested distal portion of the spicate inflorescence; specimens drying pale grayish green to dark gray; 700–2500 m elevation in Costa Rica *C. arvensis*
- 1b. Calyx 13–24 mm long, corolla 18–34 mm long; flowers short- to long-pedicellate and usually easily seen among the bracts; specimens drying grayish to blackish; 1000–3800 m in Costa Rica 2
- 2a. Leaves to 2 cm long and nearly as wide, pinnatifid with narrow (1–2 mm) central rachis and slender filiform (1 mm) pinnate lobes; clefts of the calyx tube more nearly the same (adaxial 4–6.5 mm deep, abaxial 8–12 mm deep); rarely collected, 1100–1600 m *C. tayloriorum*
- 2b. Leaves much longer than wide, usually lanceolate to linear, the pinnatifid lobes short or > 1 mm wide when present; clefts of the calyx tube differing greatly in length (adaxial 1–4 mm deep, abaxial 9–17 mm deep); rare to common, 1400–3500 m 3
- 3a. Leaves lanceolate, mostly 3–6 cm long; upper galeate lip equal to the corolla tube or up to 1.5 times as long; rarely encountered at 1400–1700 m elevation *C. lentii*
- 3b. Leaves mostly linear or pinnatifid, 1–4 cm long; upper galeate lip 2–3 times as long as the corolla tube; not collected from below 1600 m elevation [the following three species are part of a closely related complex] 4
- 4a. Plants usually densely puberulent with stiff slender whitish hairs in most parts, the stems terete or with poorly defined longitudinal ridges, parts drying dark grayish; corolla tube 7–10 mm long; uncommon in Costa Rica, 1600–3500 m *C. quirosii*

- 4b. Plants glabrous to sparsely puberulent with slender whitish hairs, the stems usually with well-defined longitudinal ridges continuous with the leaf bases, parts usually drying black; corolla tubes 7–16 mm long; commonly collected in Costa Rica, 2600–3800 m 5
- 5a. Leaves mostly entire, with short lobes near the apex; calyx red to brownish purple with yellow distal tips; 2600–3800 m in the Cordillera de Talamanca *C. talamancensis*
- 5b. Leaves usually with prominent pinnate lobes in the distal half; calyx reddish throughout; 3000–3700 m on Volcan Irazu, Volcan Turrialba, and rarely collected in the Cordillera de Talamanca ..
..... *C. irasuensis*

Castilleja arvensis Schldl. & Cham., *Linnaea* 5: 103. 1830. *C. communis* Benth. in DC., *Prodr.* 10: 529. 1846. *C. agrestis* Pennell, *Fieldiana*, Bot. 28: 519. 1953. Figure 7.

Erect **herbs**, annual, 15–80 cm tall, unbranched or with few lateral branches, leafy stems 0.7–4 mm diam., sparsely to densely hirsutulous with thin whitish hairs 0.2–1.5 mm long, gland-tipped hairs also present. **Leaves** sessile and lacking a clearly defined petiole, gradually smaller distally and intergrading with the floral bracts; **leaf blades** 15–60(–90) mm long, 4–14(–22) mm wide, oblanceolate to narrowly elliptic-obovate or elliptic, apex bluntly acute, margin entire, gradually narrowed to the cuneate base, drying greenish gray or dark gray, with thin hairs 0.2–0.5 mm long on both surfaces, tripliveined. **Inflorescences** 4–15 cm long, 2–3 cm diam., flowers subsessile and densely congested (becoming more distant in fruit), pubescent throughout with villous and glandular hairs, bracts 12–20 mm long, leaf-like to ovate-oblong, often green tipped with red or yellow, enlarging slightly in fruit, pedicels 0–1 mm long. **Flowers** hidden within the bracts, calyx 9–12 mm long, ovate-oblong and slightly curved, viscid-villous, adaxial and abaxial clefts subequal, 3–5 mm deep; **corolla** 9–12 mm long, greenish yellow, usually hidden within the calyx, tube 6–8.5 mm long, galeate upper lip 2.5–5 mm long, lower lip reduced, with 3 lanceolate lobes; ovary glabrous. **Fruits** 6–8 mm long, 3.5–5 mm wide, ovoid-oblong, dark brown, producing many seeds; seeds 0.6–1.2 mm long, 0.2–0.3 mm wide, wedge-shaped to narrowly rectangular with translucent truncated ends.

Weedy plants of moist open sunny sites in evergreen or partly deciduous forest areas, 700–2500 m elevation (to 3000 m in Guatemala). Flowering and fruiting throughout the year, but collected most often in November–March. The species ranges from central and northeastern Mexico to Paraguay; it is adventive in Hispaniola and Hawaii.

Castilleja arvensis is distinguished by its annual growth, alternate grayish leaves (when dried), densely congested spikes in which the corollas are difficult to see, green bracts often reddish at the tips, and the subsessile fruit producing numerous wedge-shaped seeds. The entire, narrowly elliptic leaves give this species a quite different appearance from Costa Rica's other *Castilleja* species. Small (3 mm) fleshy tubercle-like leaves may be present at the base of the stems near ground level. This is a well-defined species and the widest ranging of the genus; it belongs to section *Epichroma*.

Castilleja irasuensis Oersted, *Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn* 1853: 27. 1854. Figure 7.

Herbs or subshrubs, 10–50 cm tall, branching mostly from the woody base, lateral branches usually short, leafy stems 1–2 mm diam., mostly glabrous, with longitudinal ridges. **Leaves** sessile, articulated at the base, with fewer lobes distally and becoming bract-like in the inflorescence; **leaf blades** 6–30 mm long, the central portion 1–2.5 mm wide, linear and entire to pinnatifid with 1–3 pairs of lobes 0.5–8 mm long and ca. 0.8 mm wide (the longest pair often also pinnately lobed), apex bluntly acute, margin usually revolute, base with parallel margins to the stem, drying black, minutely papillate puberulent above, with larger (0.1–0.2 mm) hairs beneath, venation obscure.

Inflorescences 3–15 cm long, racemose and 1-sided, rachis hispid-villous, proximal bracts little differentiated from the leaves, distal bracts oblanceolate, ca. 2 cm long, bright red, pedicels 2–6(–11) mm long, ca. 0.3 mm diam., pubescent. **Flowers** with calyx 14–20 mm long, 4–6 mm wide, ovoid-tubular, adaxial cleft 1–4 mm deep, abaxial cleft 9–15 mm deep, lobes rounded and entire, becoming red, puberulent; **corolla** 22–30 mm long, tube 8–12 mm long, galeate upper lip 12–19 mm long, puberulent and green above, red along the mar-

gins; anthers ca. 2 mm long. **Fruits** 7–12 mm long.

Plants of open habitats in high-montane forest and paramo formations, 3000–3700 m elevation. Flowering and fruiting throughout the year. The species is endemic to the eastern volcanoes (Irazú, Turrialba) and the western part of the Cordillera de Talamanca.

Castilleja irasuensis is recognized by its restriction to high-elevation habitats, alternate pinnatifid leaves, and colorful racemes. Plants often differ because they grow on volcanic ash, open disturbed sites, or moist depressions, and the species exhibits considerable variation. More important, the characters used to separate this species from *C. talmanensis* vary greatly within and between populations. Also, the two species may hybridize in the Talamanca Mountains, and it appears that the separation of the two species may be an arbitrary distinction. This problem is worthy of careful study in the field. The name *gallito* has been recorded for this species.

Castilleja lentii N. Holmgren, Brittonia 30: 191. 1978. Figure 7.

Erect **herbs**, 20–60 cm tall, simple or branched, leafy stems 0.7–3 mm diam., with thin whitish hairs to 0.8 mm long or glabrescent, terete and with longitudinal ridges. **Leaves** sessile, often slightly thickened (articulated) at the base; **leaf blades** (1.4–)3–6 cm long, 2–7 mm wide, linear-ob lanceolate to narrowly elliptic, apex acute or slightly rounded, distal half of the margin with 1–4 short (0.7–3 mm) pairs of lateral lobes, gradually narrowed to the cuneate base, drying black, mostly glabrous above, with thin whitish hairs beneath, tripliveined from near the base. **Inflorescences** 4–9 cm long, terminal 1-sided racemes, proximal bracts leaf-like and green, distal bracts oblanceolate to obovate and distally reddish, pedicels 3–12 mm long, glabrous or pubescent. **Flowers** with calyx 12–24 mm long, 4–6 mm wide, glabrous, adaxial cleft 2–4 mm deep, abaxial cleft 12–17 mm deep, lobes usually entire, pale green below, yellow or reddish distally; **corolla** 27–33 mm long, tube 11–15 mm long, curved, galeate upper lip 12–18 mm long, 1–2 mm wide, green above and reddish along the sides, lower lip with short (1 mm) teeth. **Fruits** 9–12 mm long, 4–5 mm diam., narrowly obovoid; seeds not seen.

Plants of open sunny wet sites or moist cliff-sides in wet evergreen cloud forest formations,

1400–1700 m elevation. Flowering material has been collected in April, August, and November. The species is only known from near Cachí (Cartago Prov.) and the Río Cascajal (San José Prov.). The species is endemic to the Caribbean slope of central Costa Rica.

Castilleja lentii is recognized by its lower elevation habitat (among our species of *Castilleja*), the alternate oblanceolate leaves with short pinnate distal lobes, glabrous sepals, and long slender upper corolla lip reddish along the lateral margins.

Castilleja quirosii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1104. 1938. *C. aurantiaca* Pennell, Ann. Missouri Bot. Gard. 27: 338. 1940. *C. chiriquiensis* Pennell, loc. cit. 338. 1940. *C. seibertii* Pennell, loc. cit. 339. 1940. *C. bicolor* Pennell, loc. cit. 340. 1940. Figure 7.

Herbs or subshrubs, 30–90 cm tall, main stems with few to many branches, leafy stems 0.7–3 mm diam., terete or with poorly defined longitudinal ridges, densely hirsutulous with straight or curved hairs 0.2–0.5 mm long. **Leaves** sessile, a petiole not clearly differentiated, slightly thickened at the base (abaxially); **leaf blades** 6–30(–40) mm long, 0.7–3 mm wide (not including the lobes), linear to linear-oblong, rounded at the apex, margin entire or with 1 or 2 pairs of short (1–2 mm) narrow (0.3–0.7 mm) lobes distally, base parallel-cuneate, drying dark grayish green, densely to sparsely pubescent with stiff hairs ca. 0.2 mm long, often scabrous, venation obscure. **Inflorescences** 4–12 cm long, 1-sided racemes, rachis and bracts minutely (0.3 mm) puberulent, bracts ca. 25 mm long, 1–2 mm wide, proximal bracts leaf-like, marked with red or orange, pedicels 2–12 mm long, puberulent (sometimes with gland-tipped hairs). **Flowers** with calyx 17–20 mm long, 3–5 mm wide, minutely puberulent, red to orange or yellowish at the tip, adaxial cleft 1–3 mm deep, abaxial cleft 11–16 mm deep; **corolla** (18–)22–28(–32) mm long, yellow to yellowish green with red margin, tube 7–10 mm long, curved, galeate upper lip 15–23 mm long, ca. 1.5 mm wide, densely puberulent on the dorsal (adaxial) margin; anthers ca. 1.7 mm long. **Fruits** 8–13 mm long, 3–6 mm diam., ovoid-oblong, terminated by the persisting style base.

Plants of open sunny sites or partly shaded sites in evergreen montane and open paramo formations, 1600–3500 m elevation. The species appears to do best in volcanic soils and burnt areas. Flowering and fruiting throughout the year. The

species ranges from Volcan Irazú eastward to the Chiriquí highlands of Panama.

Castilleja quirosii is recognized by its generally dense short pubescence, small alternate linear leaves with few short distal lobes, colorful flowers in one-sided racemes, and unusual corollas. Among our species of *Castilleja*, this species has the widest altitudinal range within Costa Rica, although it is not frequently collected. This species and its close congeners should be studied in the field; it seems possible that *C. quirosii* might be included within a more broadly defined *C. irasuensis*.

Castilleja talamancensis N. Holmgren, Brittonia 30: 187. 1978.

Herbs and shrubs, erect or clambering, 0.1–1.5(–2) m tall, simple or with many distal branches, woody at the base, stems 0.8–3.5 mm diam., glabrous or minutely (0.1 mm) puberulent, with prominent longitudinal ridges. **Leaves** sessile or subsessile, slightly articulated at the base, bract-like at the base of the inflorescence; **leaf blades** 5–18(–25) mm long, 0.5–2 mm wide, linear to linear-oblong, often with short distal lateral lobes 0.5–1.5 mm long, apex rounded, margins entire or with small lobes near the apex, base decurrent on the stem, drying black, glabrous or minutely (0.05 mm) puberulent beneath, venation obscure. **Inflorescences** 2–8 cm long, 1-sided racemes, rachis minutely hispidulous, proximal bracts leaf-like, distal bracts obovate with rounded apex, marked with red, purple, or green, pedicels 2–11 mm long, 0.2–0.4 mm diam., with erect thin hairs 0.1–0.2 mm long. **Flowers** with calyx 14–20 mm long, 3–4 mm diam., adaxial cleft 1–3.5 mm deep, abaxial cleft 9–17 mm deep, rounded at the apices, minutely puberulent along the veins, red to brownish purple with yellow distal margin; **corolla** 20–32 mm long, tube 7–12 mm long, hooded upper lip 13–22 mm long, green above, margins red to orange, lower lip reduced with 3 narrow teeth ca. 1 mm long. **Fruits** 6–9 mm long, 4–5 mm diam., dark brown and smooth; seeds ca. 2 mm long, C-shaped.

Plants of open or partly shaded sites in highmontane forest and paramo formations, 2600–3800 m elevation. Flowering and fruiting throughout the year. The species is endemic to the Cordillera de Talamanca of Costa Rica.

Castilleja talamancensis is recognized by its restriction to higher elevations, narrow linear-oblong leaves that may have three small lobes at the

apex, and the colorful inflorescences. The distal bracts subtending undeveloped flowers are often bright red. Plants in protected sites become large and shrubby, while those on exposed ridges or open sites are small and have few branches. This species is particularly successful along the disturbed margins of the Carretera Interamericana. However, there is so much variation in this species, and within *C. irasuensis* and *C. quirosii* as well, that there is the strong possibility that all three would be better considered a single variable species, with *C. irasuensis* having priority. Careful field work with the living populations should help resolve this problem. The name *flor de Indio* has been used for this species.

Castilleja tayloriorum N. Holmgren, Brittonia 30: 193. 1978.

Slender herbs, annual or short-lived perennials, erect, 25–150 cm high, stems 0.4–1.5 mm diam., glabrous or with few minute (0.1 mm) appressed whitish hairs. **Leaves** sessile or appearing to have winged petioles (to the first lobes), deeply pinnatisect from a narrow (0.7–2 mm) rachis; **leaf blades** 5–20 mm long, 3–14 mm wide, with a slender (petiole-like) proximal half and the distal rachis bearing 2 or 3 pairs of narrow (1–2 mm) lateral lobes, the proximal lobes often with smaller distal lobes, apices rounded, margin entire and revolute, drying dark grayish, glabrous, venation obscure. **Inflorescences** 3–7 cm long, racemes (often 1-sided), lower bracts leaf-like and green, distal bracts shorter and reddish, often deciduous, pedicels 3–8 mm long, ca. 0.4 mm diam., minutely puberulent. **Flowers** with calyx 13–17 mm long, glabrous, adaxial cleft 4–6.5 mm deep, abaxial cleft 8–12 mm deep, major lobes usually rounded and yellowish; **corolla** 22–25 mm long, curved, tube 8–12 mm long, ca. 1 mm diam., curved, galeate upper lip 13–15 mm long, finely puberulent and green dorsally, margins reddish, lower lip short. **Fruits** 7–10 mm long, ca. 4 mm wide, obovoid or oblong with abruptly truncated apex.

Plants of open sites or cliffsides in wet evergreen cloud forest formations, 1100–1600 m elevation. Flowers were collected in August and October, fruiting in October. The species is known from only two collections: *Gómez-Laurito 10180*, from near the highway tunnel at Zurquí, and *J. Taylor & C. Taylor 11901*, from below Bajo La Hondura. Presently the species is only known from the upper Río Zurquí drainage in Braulio

Carrillo National Park on the Caribbean slope of central Costa Rica.

Castilleja tayloriorum is recognized by its lower elevation habitat, small pinnatifid leaves with slender lateral lobes, glabrous calyx, slender curved corolla tube, and long narrow upper lip. *Castilleja tayloriorum* is probably most closely related to species of section *Epichroma* from south-central Mexico.

Cymbalaria Hill

REFERENCES—G. Cufodontis, Die Gattung *Cymbalaria* Hill. Nachtrage und Zusammenfassung. Bot. Not. 1947: 135–156. 1947. D. Sutton, A Revision of the Tribe Antirrhineae. British Museum (Natural History) & Oxford Univ. Press. 1988.

Weak-stemmed **herbs**, creeping or twining, perennials, simple or much-branched. **Leaves** opposite or alternate, simple, long-petiolate, leaf blades reniform to suborbicular, palmately lobed or toothed, venation palmate. **Inflorescences** racemes, cymes, or solitary flowers in leaf axils, pedicels well developed, elongating in fruit, bracteoles absent at the base of the calyx. **Flowers** small, calyx united only at the base, sepals 5, imbricate (valvate) in bud, enlarging slightly in fruit; **corolla** strongly bilabiate, usually blue or purple, tube with a short, backward-pointing abaxial spur at the base, upper lip with 2 lobes, lower lip with 3 lobes and elevated transverse ridge (upper palate) restricting access to the throat; stamens 4, of 2 unequal pairs, included, thecae separate and parallel; ovary 2-locular, ovules many, stigma 2-lobed. **Fruits** dry capsules, opening by 2 pore-like slits, the 2 valves often splitting into 3; seeds ellipsoid or crested, rugulose.

A genus of nine species native to western European and the Mediterranean. It is classified in the tribe Antirrhineae, and its species were once placed in *Linaria*, but they differ in having solitary axillary flowers and leaves with palmate venation. Several species are used in ornamental horticulture as groundcover and in hanging baskets. One adventive species is sometimes found on moist walls in Mexico and Central America.

Cymbalaria muralis P. Gaertn., B. Meyer & J. Sherb., Oekon. Fl. Wetterau 2: 397. 1800. *Antirrhinum cymbalaria* L., Sp. Pl., 612. 1753.

Linaria cymbalaria (L.) Miller, Gard. Dict., ed. 8, #17. 1768.

Herbs with slender creeping or pendent stems, often rooting from the nodes, internodes 0.5–1.0 cm long, 0.5–1.7 mm diam., glabrous. **Leaves** mostly alternate, glabrous, petioles 10–45 mm long, 0.3–0.5 mm diam.; **leaf blades** 10–35 mm long, 9–40 mm wide, orbicular-oblate to reniform in outline, apex obtuse to rounded with apiculate tip, margins entire with usually 5 (3, 7) rounded lobes separated by short narrow sinuses, base subcordate to deeply cordate, drying dark greenish or grayish, with usually 3 major veins. **Inflorescences** of solitary axillary flowers, pedicels 12–40 mm long, 0.4–0.7 mm diam., glabrous, elongating to 6 cm and negatively phototropic after anthesis. **Flowers** glabrous externally, sepals 0.8–1.5 mm long, 0.5–0.8 mm wide, lanceolate to narrowly oblong, elongating to 2.5 mm long in fruit; **corolla** 7–9 mm long, lilac or pale violet to blue with yellow interior, tube 3.5–4 mm long (including the spur to 2 mm long), lower lip ca. 3 mm long. **Fruits** 2.7–4 mm long, 3–4 mm wide, globose or rounded-oblong, thin-walled.

Cymbalaria muralis, as its Latin epithet implies, is usually found on damp shaded walls. A native of Europe, this species has only been collected in San José and Tres Ríos (1100–1300 m) in Costa Rica. The slender stems, small thin-textured five-lobed cordate leaves, and solitary flowers with strongly bilabiate bluish corolla and backward-oriented spur make these plants quite distinctive. In addition, the pedicels are negatively phototropic after anthesis, moving the capsules into dark corners as they elongate. They are sometimes planted as cover plants in gardens and are called Kenilworth ivy, Coliseum ivy, and pennywort.

Darcya Turner & Cowan

REFERENCE—B. Turner & C. Cowan, *Darcya* (Scrophulariaceae), a new genus from Central and South America. Phytologia 74: 267–270. 1993.

Herbs or weak-stemmed subshrubs to 1 m tall, annual or perennial, glabrous or puberulent, drying greenish to dark brown. **Leaves** opposite, simple, petiolate, blades with serrulate margins, venation pinnate or subpalmate with 3–5 major veins from near the base. **Inflorescences** terminal racemes with 2 flowers/node separated by well-

developed internodes (flowers solitary in axils of distal leaves or bracts), pedicels slender, bracteoles absent at the base of the calyx. **Flowers** with calyx deeply 5-parted, calyx lobes equal or subequal, valvate in bud, enlarging slightly in fruit; **corolla** tubular and strongly 2-lipped (bilaterally symmetric), white to blue or purple, tube shorter than the lips, lower (abaxial) lip 3-lobed and larger, upper (adaxial) lip 2-lobed; stamens 4, subequal or unequal, filaments borne at 2 levels on the corolla tube, anthers with straight white hairs on dorsal side; ovary ovoid, style short. **Fruits** thin-walled capsules, dehiscence loculicidal and sep-

tidal producing 4 valves (or irregular); seeds small, oblong to trapezoidal, testa reticulate.

Darcya is a genus of three narrowly endemic species, restricted (respectively) to Costa Rica, Panama, and Colombia. These plants resemble species of *Stemodia* but differ in having pubescent anthers, very short styles, more clearly racemose inflorescences, three or five prominent veins from the base of the blade, and oblong trapezoidal seeds. The decurrent leaf bases merge with the longitudinal ridges (angles) of the stem in a distinctive manner. This genus also resembles the Asiatic genus *Limmophila*, which has become an invasive weed in some areas.

Key to the Species of *Darcya*

- 1a. Calyx and pedicels glabrous; leaf blades 15–45 mm long, ovate-triangular to ovate-elliptic; stamens 4, subequal; plants of the wet Caribbean slope in central Costa Rica *D. costaricensis*
- 1b. Calyx and pedicels puberulent; leaf blades 17–60 mm long, ovate-lanceolate; stamens 4 in 2 unequal pairs; collected in the area of Boquete, Chiriquí, Panama *D. reliquiarum*

Darcya costaricensis (B. L. Turner) B. L. Turner, *Phytologia* 74: 268. 1993. *Stemodia costaricensis* B. L. Turner, *Phytologia* 73: 253. 1992. Figure 3.

Erect or sprawling **herbs** to 1 m tall with many internodes 3–6 cm long, leafy stems 0.7–2.5 mm diam., glabrous, terete but with 4 longitudinal ridges, nodes without an interpetiolar ridge. **Leaves** opposite, petioles 2–10 mm long, 0.4–1.2 mm wide, lateral margins decurrent on the stem and continuous with the stem ridges; **leaf blades** 15–45 mm long, 10–25 mm wide, ovate-triangular to ovate-elliptic, apex acute, margin with 4–6 teeth/cm, often revolute (dried), base obtuse to truncate, minutely punctate, glabrous or with few minute (0.1 mm) hairs beneath, subpalmate with 3 prominent basal veins, 2° veins 2 or 3/side. **Inflorescences** 5–10 cm long, glabrous racemes, basal flower pair subtended by reduced leaves (12–16 mm long), distal flowers subtended by sessile lanceolate or linear bracts 2–6 mm long, pedicels 6–16 mm long, glabrous. **Flowers** glabrous externally, calyx lobes 2.5–3 mm long, to 4 mm in fruit, 0.3–0.5 mm wide, narrowly oblong, apex truncated and thickened, with 3 prominent parallel veins; **corolla** 4–7 mm long, blue or purple, tube 3–4 mm long, puberulent internally near the mouth, central lobe of lower lip 3–6 mm long; stamens 4, subequal, anthers similar; stigma in-

cluded. **Fruits** 3–4 mm long, 1.5–2 mm wide, narrowly ovate to oblong, persisting style 0.4–0.8 mm long; seeds 0.5–0.7 mm long, yellowish brown, reticulate with longitudinal ridges separated by rounded pits.

Plants of open sites and along stream edges in very wet lower montane forest formations of the Caribbean slope, 1400–1600 m elevation. Flowering and fruiting throughout the year. This species is known only from along the upper Río Grande de Orosí, Tapantí Refuge, Cartago Province, central Costa Rica.

Darcya costaricensis is recognized by its weak-stemmed herbaceous habit, opposite leaves with broad serrulate blades, racemose inflorescences, narrow calyx lobes, two-lipped blue or purple corollas with short tube, and restricted geographical range. This material had earlier been placed in *Stemodia reliquiarum* (see the following species).

Darcya reliquiarum (D'Arcy) B. L. Turner & C. C. Cowan, *Phytologia* 74: 269. 1993. *Stemodia reliquiarum* D'Arcy, *Ann. Missouri Bot. Gard.* 66: 258. 1979.

Herbs with sprawling stems to 40 cm tall, leafy stems 0.7–3 mm diam., with 2 prominent ridges, glabrous except near the nodes with erect 5-celled hairs, glabrescent, drying brown. **Leaves** opposite, petioles 0–4(–8) mm long, with narrow lat-

eral margins decurrent on the stem and poorly differentiated from the blade; **leaf blades** 1.7–6 cm long, 10–26 mm wide, ovate-lanceolate to narrowly ovate, apex acute, margins serrulate distally with 10–15 teeth/side, base obtuse or truncate, punctate on both surfaces, glabrous, subpalmate with 3 major veins from the base, midvein with 2 or 3 lateral veins/side. **Inflorescences** terminal open racemes, rachis 0.5–0.8 mm diam., bracts leaf-like to scale-like, mostly linear (ca. 3 × 1 mm), ciliolate along the edge with multicellular gland-tipped hairs 0.1–0.3 mm long, pedicels 4–12 mm long, puberulent. **Flowers** small, calyx lobes 2–4 mm long, ca. 0.5 mm wide, minutely puberulent externally, with 3 longitudinal veins, drying brown; **corolla** 4–6 mm long, salverform, blue to lavender or purple, tube 3–4 mm long, slightly exceeding the calyx, subglabrous externally, lobes 2–3 mm long, subequal, minutely puberulent at the base within; stamens 4, the lower 2 filaments ca. 0.5 mm long and with reduced thecae, the upper filaments 0.7–1 mm long, inserted near the middle of the tube, one theca sessile on the connective with the other on a stipe-like arm of the connective; ovary conical, style 0.5 mm long, stigma club-like. **Fruits** 4–5 mm long, 2.4–3 mm wide, dehiscent apically into 4 valves, placenta broad, unwinged; seeds many, 0.4–0.6 mm long, oblong to trapezoidal, longitudinally reticulate, dark brown.

Plants of evergreen montane cloud forests around Boquete, 1500–2500 m elevation. Probably flowering throughout the year. Endemic to the Chiriquí highlands of western Panama.

Darcya reliquiarum is recognized by its herbaceous sprawling habit, opposite serrulate leaves with subpalmate venation, racemose puberulent inflorescences, narrow calyx lobes, strongly 2-lipped blue or purple corolla, pubescent anthers, and restricted geographical range.

Digitalis Linnaeus

REFERENCE—K. Werner, Zur Nomenclature und Taxonomie von *Digitalis* L. Bot. Jahrb. Syst. 79: 218–254. 1960.

Erect **herbs** or rarely shrubs, biennial or perennial, stems simple or branched from the base. **Leaves** alternate, sessile or petiolate, entire to dentate, pinnately veined, drying greenish or grayish. **Inflorescences** terminal racemes, the flowers often aligned along one side, bracts sub-

tending the pedicels, lacking bracteoles at the base of the calyx. **Flowers** large and colorful, calyx with 5 sepals united only near the base, imbricate in bud, enlarging slightly in fruit; **corolla** tubular to campanulate, longer than the calyx, purple to yellow or white, bilaterally symmetric with the lower lip slightly longer than the upper, upper lip entire or 2-cleft, lower lip 3-lobed, lateral lobes exterior in bud; stamens 4 in 2 similar pairs, included within the tube, anthers with 2 divergent thecae; ovary 2-locular, ovules many, style simple, stigma 2-lobed. **Fruits** dry capsules, dehiscent septically; seeds many, minute, rugulose.

Digitalis is a genus of about 20 species ranging from western Europe into central Asia. They are classified in the subtribe Digitalieae of the tribe Veroniceae and are distinguished by their erect habit, one-sided racemes, and large tubular corollas. The common foxglove is found in gardens and as an escape in the cooler highlands of Central America.

Digitalis purpurea L., Sp. Pl. 621. 1753. Figure 8.

Stout **herbs**, 0.5–1.8 m tall, biennial, leafy stems 2–8 mm diam., minutely puberulent with thin hairs 0.1–0.3 mm long. **Leaves** becoming progressively shorter from base to inflorescence, petioles 1–11 cm long but not well differentiated from the blade, 2–12 mm wide with winged margins; **leaf blades** 2.5–20 cm long, 1–8 cm wide, narrowly elliptic to ovate-elliptic or elliptic-obovate, apex acute to obtuse, margin serrate with 5–10 teeth/cm, gradually narrowed to the cuneate base, minutely puberulent on both surfaces, 2° veins 3–5/side, strongly ascending. **Inflorescences** 15–40 cm long, flowers mostly along 1 side, bracts 8–18 mm long, lanceolate, sessile, pedicels 5–10 mm long, 0.4–0.7 mm diam., puberulent. **Flowers** with calyx 8–16 mm long, sepals separate to the base, 4–7 mm wide, broadly ovate to ovate-oblong, ciliolate along the edge; **corolla** 20–50 mm long, tube 1.3–2 cm wide, tubular-campanulate, pink to purple (white), lower lip extending 3–8 mm beyond the upper lip, usually with dark spots within the throat; thecae divergent and equal, ca. 3 mm long. **Fruits** 9–11 mm long, 9–10 mm diam., ovoid with broadly truncated base, minutely puberulent; seeds 0.4–0.7 mm long, narrowly rectangular.

Digitalis purpurea, native to Europe, occurs as a garden plant and in small naturalized populations in high-montane areas, 1800–3300 m elevation. This species is distinctive, with its alter-

nate leaves gradually narrowed into the long petiole, conspicuous (often one-sided) racemes of large colorful flowers, and the open corolla tubes marked with dark spots within. Many varieties are used in ornamental horticulture. The plants are poisonous to livestock and contain a number of potent compounds. This species is the principal source of digitalin, an important drug in treating some kinds of heart ailments. Common names are *digital*, *manga de la Señora*, and foxglove.

Escobedia Ruiz & Pavón

REFERENCES—F. Pennell, *Escobedia*, a Neotropical genus of Scrophulariaceae. Proc. Acad. Nat. Sci. Philadelphia 83: 411–426. 1931. J. Thieret, The Scrophulariaceae—Buchnereae of Central America. Ceiba 8: 92–101. 1961.

Perennial **herbs**, stems simple or branched, glabrous or puberulent, striate or angled, roots yellow to orange. **Leaves** opposite, sessile or subsessile, base cuneate to clasping, coriaceous, entire to serrulate, venation pinnate to subpalmate, often scabrous. **Inflorescences** racemose or with solitary flowers in axils of distal leaves, pedicels (peduncles) with 2 bracteoles distally or lacking bracteoles. **Flowers** large, calyx tubular to funnelform, with 5–10 longitudinal veins, lobes 3–6, shorter than the tube, triangulate to rounded; **corolla** salverform with a long slender tube, usually white, externally glabrous or puberulent, lobes 5, small to large, equal and rounded; stamens 4, subequal, inserted in the middle of the tube, filaments ciliate or glabrous, anthers glabrous and aristate; ovary 2-locular, ovules many, style elongate, stigmas linear on the side of the style apex. **Fruits** dry capsules, ellipsoid, hard, included within the persisting calyx; seeds many, narrowly conical to linear-oblong, surface reticulate.

Escobedia is a genus of six to eight species ranging from Mexico to Bolivia and Brazil. The genus is classified in the tribe Buchnereae, subtribe Melasmineae. These plants are distinctive among Neotropical Scrophulariaceae because of their large salverform white corollas with long narrow tubes. The roots have been used by indigenous peoples as a source of a yellow dye for food coloring. Three species are found in northern Central America (Standley & Williams, 1973), but only one of these has been found in Costa Rica. *Escobedia laevis* Schldl. & Cham. (with long linear leaves and calyx 4–7 cm long with narrow

calyx lobes) ranges from southern Mexico to central Nicaragua.

Escobedia grandiflora (L.f.) O. Kuntze, Rev. Gen. Pl. 3: 231. 1893. *Buchnera grandiflora* L.f., Suppl. Pl. 287. 1781. *E. scabrifolia* Ruiz & Pavón, Syst. Veg. Peruv. Chil. 159. 1798. *Micalia grandiflora* (L.f.) Raf., Fl. Tell. 2: 104. 1837. *E. curialis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 83: 417. 1931. *E. longiflora* Pennell, loc. cit. 423. 1931. *E. reticulata* Pennell, loc. cit. 420. 1931. Figure 6.

Erect perennial **herbs**, 0.6–1.5(–2) m tall, leafy stems 1.5–7 mm diam., with stiff whitish hairs 0.1–0.3 mm long, smooth or scabrous, roots bright yellow-orange. **Leaves** opposite or subopposite, gradually becoming smaller distally, subsessile with petioles 1–4 mm long, ca. 2 mm wide; **leaf blades** 5–12 cm long, 1.5–3 cm wide, lanceolate to narrowly triangular or ovate-elliptic, apex acute, margin serrate with 1–3 teeth/cm, base rounded and truncate to auriculate, drying pale to dark gray and coriaceous, scabrous above and below with short (0.1–0.2 mm) hairs, tripliveined from the base or palmately 5-veined. **Inflorescences** of solitary flowers (2/node) in axils of smaller distal leaves (or the inflorescences racemose if the smaller leaves are interpreted as bracts), pedicels 11–35 mm long, 0.7–2 mm diam., slightly curved, often with linear bracteoles to 4 mm long in the upper third. **Flowers** with calyx 34–44 mm long, 6–10 mm diam., scabrous, lobes 2–5 mm long, triangular; **corolla** 7–12 cm long, 6–8 cm wide at the mouth, salverform with a long narrow tube to 10 cm long, 3–8 mm diam., lobes 1–3 cm long and broadly rounded, white, minutely puberulent; stamens inserted on the middle of the tube; ovary glabrous, style 5–8 cm long. **Fruits** 20–28 mm long, ca. 10 mm wide, smooth; seeds 3–4 mm long, 0.3–0.5 mm wide, linear-rectangular, translucent except for the center.

Uncommon plants of open sites, in marshy or wet situations of lower montane evergreen forest formations, 1000–1500 m elevation. Collected in flower in July–February. The species ranges from Mexico to Brazil.

Escobedia grandiflora is recognized by its opposite scabrous coriaceous subsessile leaves with three (five) major veins, distal nodes with two large opposite flowers, and large white corollas with long narrow tubes and widely flaring limb. The color, form, and size of the corolla suggest nocturnal pollination by hawkmoths. *Escobedia*

reticulata (from near Canas Gordas, Pittier 11118 holotype US) was distinguished by Pennell and Thieret on the basis of a pustulate calyx and the size and position of the bracteoles. This is most likely a local variation and not deserving of species rank (D'Arcy, 1979, p. 220).

Gerardia species are now placed in *Agalinis* (q.v.).

Gibsoniothamnus is now placed in the Schlegeliaceae.

Hemichaena Bentham

REFERENCE—J. Thieret, Synopsis of *Hemichaena*, including *Berendtiella* (Scrophulariaceae). Fieldiana, Bot. 34: 89–99. 1972.

Herbs or shrubs, simple or branched, glabrous or viscid-pubescent, drying brownish. **Leaves** opposite or fasciculate, sessile or subsessile, margins dentate, surface often rugose, venation pinnate. **Inflorescences** axillary, of solitary flowers or 1 or 2 cymes/axil, usually pedunculate with bracts subtending the well-developed pedicels, bracteoles absent at the base of the calyx. **Flowers** showy, calyx campanulate to tubular, with 5 prominent longitudinal costae, 5-lobed or 5-toothed, lobes unequal, shorter than the tube; **corolla** funnelliform to tubular-campanulate, 2-lipped, bright yellow to orange or red, tube exceeding the calyx, lobes equal to or shorter than the tube, upper lip 2-lobed or emarginate, lower lip 3-lobed; stamens 4, subequal or of 2 unequal pairs, included or exserted, inserted at the middle or on the lower half of the tube, anthers 2-locous, parallel but becoming divergent, staminode absent; ovary 2-locular, placentas bilamellate, ovules many, style slender, with 2 flattened stigmatic areas or lobes at the apex. **Fruits** dry capsules, ovoid to oblong, loculicidally dehiscent and secondarily septicidal; seeds very many, minute, linear-oblong to fusiform, testa reticulate with thin translucent walls.

A genus of five species, ranging from northern Mexico to the Talamanca mountains of Costa Rica. *Hemichaena* is classified in the tribe Dodartieae, with *Mimulus*, *Mazus*, *Leucocarpus*, and *Berendtiella*. The genus was monotypic, but Thieret (1972, cited above) broadened the concept to include the four species of *Berendtiella*. Generic delimitations within the tribe are problematic. If characters of the fruit are emphasized, then

Hemichaena and *Berendtiella* appear closely related, but *Hemichaena* can be distinguished by its amplified corolla tube, included stamens that are attached near the base of the corolla, and cordate-amplexicaul leaves. The generic classification of the tribe Dodartieae will remain obscure until *Mimulus* is revised and the classification of the entire group is compared. Only the following disjunct species is found south of northern Nicaragua.

Hemichaena fruticosa Benth., Pl. Hartw. 78. 1841. *Leucocarpus fruticosus* (Benth.) Benth. in DC., Prodr. 10: 336. 1846.

Herbs or shrubs to 2 m tall, distal stems with few or no lateral branches, leafy stems 2–11 mm diam., terete or slightly quadrangular, densely pubescent with gland-tipped hairs 0.5–1.3 mm long. **Leaves** opposite, sessile, of similar size along the stems, equal or subequal at the node; **leaf blades** 5–17 cm long, 2–5 cm wide, lanceolate to narrowly elliptic-lanceolate or oblanceolate, apex acute or acuminate, margin serrate with 3–6 small or prominent teeth/cm, base rounded and auriculate to cordate-amplexicaul, drying dark above and paler beneath, minutely glandular puberulent with hairs 0.2–0.6 mm long, 2° veins 4–9/side. **Inflorescences** 3–8 cm long, usually of 1 or 2 axillary cymes (1–4/node), peduncles 10–28 mm long, bracts 6–22 mm long, 1–5 mm wide, lanceolate, viscid puberulent with hairs ca. 0.5 mm long, pedicels 5–18 mm long. **Flowers** with calyx 11–16 mm long, 4–6 mm diam., densely puberulent with gland-tipped hairs, lobes 3–8 mm long, narrowly triangular and acute; **corolla** 25–45 mm long, 14–28 mm wide at the mouth, tubular-campanulate, tube 6–11 mm wide at the mouth, minutely puberulent externally, lobes 5–9 mm long; stamens subequal, inserted in the lower ¼ of the tube, filaments 12–15 mm long, glabrous, anthers 3.3–3.8 mm long; style 15 mm long, stigmas flattened. **Fruits** 13–17 mm long, 4–6 mm diam., oblong, becoming brown; seeds 0.6–1 mm long, 0.3–0.4 mm wide, narrowed at each end.

Plants of open moist to wet sunny sites along streams, on steep slopes, and in disturbed sites in montane evergreen forest formations, 1600–3100 m elevation. Probably flowering and fruiting throughout the year, but collected most often in December–March. The species is found in southern Mexico and Guatemala and in the western portion of the Cordillera de Talamanca.

Hemichaena fruticosa is recognized by its stout viscid puberulent stems, sessile opposite serrate

leaves, axillary cymes, bright yellow corollas that are only slightly bilabiate, and its restricted geographical range (in Costa Rica). It is surprising that this species, which is so common in the western half of the Cordillera de Talamanca, has not been collected elsewhere in Costa Rica. D'Arcy (1979) placed this species in synonymy under *Leucocarpus perfoliatus* (H.B.K.) Benth., but that species has smaller flowers, smaller leaves, and baccate white fruits.

Lamourouxia Kunth in H.B.K.

Nomen conservandum

REFERENCE—W. Ernst, Floral morphology and systematics of *Lamourouxia* (Scrophulariaceae: Rhinanthoideae). *Smithson. Contrib. Bot.* 6: 1–63. 1972.

Perennial **herbs** or subshrubs, usually woody at the base, stems erect or scandent, distal stems often few-branched and arched, glabrous or pubescent, gland-tipped hairs often present, probably hemiparasitic on roots. **Leaves** opposite (verticillate), sessile or short-petiolate, often smaller and bract-like distally, blades serrate to deeply dissected, drying brownish or black, pubescent with simple, branched, or gland-tipped hairs. **Inflorescences** of solitary flowers in distal leaf axils (1 or 2/node) or appearing racemose (paniculate or corymb-like) when distal leaves are bract-like, pedicels ebracteolate at the apex. **Flowers** large and showy, calyx tubular-campanulate, 4-lobed, lobes subequal or of 2 unequal pairs (rarely cleft to

base), obtuse to deltoid or linear, with 10 prominent longitudinal veins; **corolla** tubular and bilabiate, red to orange or white, usually puberulent on the exterior, upper lip often erect (rarely hood-like), entire or bilobed, lower lip usually shorter, narrow, 3-lobed, biplicate within below the apex; **stamens** 4 in 2 subequal pairs or with 2 fertile stamens and 2 staminodes, attached near base of corolla tube, filaments swollen and puberulent at the base, included in the upper lip, fertile anthers basifixed and pilose; ovary 2-locular, ovules many, stigma terminal, exerted and 2-lipped. **Fruits** dry capsules, ovoid to ellipsoid with persisting style-base, opening loculicidally into 2 entire valves; seeds many, ellipsoid to oblong, minutely bullate to reticulate.

Lamourouxia is a genus of ca. 24 species found in Neotropical highlands from Mexico to Peru. The center of species richness is in Mexico, with only three species found in southern Central America and two species in the Andes. Although a very distinctive genus, the individual species can be difficult to separate from each other. In Costa Rica the plants are restricted in distribution and not often collected. The large showy flowers with bright red or orange narrowly tubular corollas, spicate or racemose inflorescences, four-lobed calyx, subsessile leaves, and preference for open habitats at mid-elevations help distinguish this genus. Our species belong to section *Hemispadon*, according to Ernst's fine monograph (1972, cited above). *Lamourouxia* is in the subfamily Rhinanthoideae. Every member of this subfamily that has been tested is hemiparasitic, perhaps explaining why these lovely plants are not seen in gardens.

Key to the Species of *Lamourouxia*

- 1a. Calyx glabrous; young stems glabrous except for longitudinal lines of minute hairs; leaves linear-lanceolate; 1600–2800 m elevation *L. lanceolata*
- 1b. Calyx puberulent externally; young stems pubescent; leaves narrowly elliptic to ovate-triangular; 900–1800 m elevation 2
- 2a. Stems and flowers with simple (non-gland-tipped) hairs, leaves 7–24 mm long; flowering mostly November–February *L. gutierrezii*
- 2b. Stems and flowers with gland-tipped hairs; leaves 10–110 mm long; flowering in July–December *L. viscosa*

Lamourouxia gutierrezii Oerst. in Benth. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1853: 29. 1853. *L. scabra* Seemann, Bot. Voy. Herald 177: pl. 33. 1854. Figure 5.

Herbs or subshrubs, 0.5–1.3(–2) m tall, distal branches arched and often with short lateral branching, leafy stems 1–4 mm diam., sparsely to densely puberulent with thin straight or retrorse hairs 0.2–0.5 mm long. **Leaves** opposite (verticillate), sessile or subsessile with poorly differentiated petioles to 2 mm long; **leaf blades** 7–24 mm long, 2–10 mm wide, elliptic to elliptic-oblong or ovate-elliptic, apex obtuse or rounded, margin with 4–6 rounded teeth/cm, base cuneate, drying dark grayish green, slightly scabrous above and below with short stiff hairs ca. 0.2 mm long, 2° veins 3–5/side. **Inflorescences** 5–20 cm long, spicate or racemose, bracts 8–12 mm long, 5–6 mm wide, leaf-like and lanceolate to ovate, sometimes caducous and the flowers appearing ebracteate, pedicels 2–5 mm long, ca. 0.7 mm diam., puberulent. **Flowers** with calyx 6–9 mm long, enlarging to 12 mm in fruit, 2–4 mm diam., cupulate, 5-lobed, lobes 2–4 mm long, triangular to lanceolate; **corolla** 30–44 mm long, 4–6 mm diam., tubular, bright red to orange-red, densely puberulent externally, upper lip ca. 14 mm long; functional stamens 2, anthers connivent and positioned against the upper lobe, 3–4 mm long with hairs 1–2 mm long; ovary glabrous, style 2–4 cm long. **Fruits** 8–13 mm long, 4–8 mm diam., ovoid, short-beaked, dark and smooth; seeds 0.8–1 mm long, 0.3–0.4 mm thick.

Infrequently collected plants of open sites in lower montane evergreen forest formations, 900–1900 m elevation. Probably flowering throughout the year, with most collections made in November–February and June–July. The species ranges from the western part of the Meseta Central in Costa Rica to the Chiriquí highlands in Panama.

Lamourouxia gutierrezii is recognized by its smaller narrow scabrous leaves, simple pubescence, and puberulent calyx. The structure and position of the staminodes suggest that they may function as a barrier to keep visiting insects from the ovary. This is the only species of the genus endemic to southern Central America.

Lamourouxia lanceolata Benth. in DC., Prodr. 10: 542. 1846. *L. longiflora* var. *lanceolata* (Benth.) L. O. Williams, Fieldiana, Bot. 34: 121. 1972. Figure 5.

Herbs or subshrubs to 1.5(–3) m tall, erect or scandent, stems often arching and with multiple branching, leafy stems 1–3 mm diam., with minute (0.2 mm) crooked hairs in 2 opposing longitudinal lines along the stems. **Leaves** sessile or subsessile with poorly defined petioles to 2 mm long, not conspicuously smaller distally; **leaf blades** 11–48(–57) mm long, 2–8(–14) mm wide, narrowly lanceolate to narrowly linear-lanceolate or narrowly elliptic-oblong, apex acute, margin with 4–6 teeth/cm, base narrowly cuneate, drying brownish to blackish, glabrous or with minute (0.1 mm) papillate-puberulent hairs on the midvein above, 2° veins 4–7/side. **Inflorescences** 3–15 cm long or of flowers axillary to distal leaves, flowers subtended by leaves very similar to those lower on the stems, pedicels 3–9(–14) mm long, 0.4–0.8 mm diam., glabrous or with a line of hairs along one side. **Flowers** with calyx 7–18 mm long, 3–5 mm diam., glabrous externally, veins elevated, lobes 6–15 mm long and becoming reflexed; **corolla** 25–47 mm long, 4–7 mm diam., tubular, bright red to red-orange, densely puberulent externally, upper lip 14–18 mm long; stamens 2, with larger pubescent anthers often coherent, staminodes 2, borne above the fertile stamens, thickened at the apex. **Fruits** 8–14 mm long, 5–8 mm diam., ovoid-rounded, beaks 1–2 mm long; seeds 1–1.3 mm long, oblong to wedge shaped, surface reticulate.

Infrequently collected plants of open sites in evergreen montane forest formations, 1600–2800(–3200) m elevations. Flowering in December–March. In Costa Rica this species is known only from the western portion of the Cordillera de Talamanca. The species ranges from central Mexico to Costa Rica.

Lamourouxia lanceolata is recognized by its narrow opposite leaves, glabrous calyx with reflexed lobes, narrow bright red corolla tubes, androecium of two stamens with pubescent anthers and two staminodes, and higher elevation habitats. This species has been confused with *L. longiflora* Benth. (Williams, 1972; Standley & Williams, 1973), but *L. longiflora* has four fertile stamens and the calyx is puberulent on the exterior.

Lamourouxia viscosa Kunth in H.B.K., Nov. Gen. Sp. 2 ed., folio 272. 1817; ed. quarto 338. 1818. *L. vejizensis* Oerst. in Benth. & Oerst., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1853: 28. 1853.

Erect perennial **herbs** 0.5–1.3(–3) m tall, leafy stems 1.5–7 mm diam., terete, densely puberulent with gland-tipped hairs 0.2–0.7 mm long. **Leaves** gradually diminishing in size distally, sessile or subsessile with petioles ca. 1 mm long, appearing amplexicaul; **leaf blades** 1–7(–11) cm long, 6–28(–53) mm wide, ovate-triangular to narrowly triangular-oblong, apex acute, margin serrate with 2–6 teeth/cm, base truncate to cordate-auriculate and amplexicaul, drying dark grayish to dark brown and coriaceous, with short (0.3 mm) hairs above and more densely puberulent beneath, 2° veins 3–7/side. **Inflorescences** 10–20 cm long, racemes or spicate, glandular puberulent, flowers crowded or separated by internodes to 12 mm long, bracts 5–16 mm long, 3–11 mm wide at the base, ovate to lanceolate, sessile, pedicels 1–3(–6) mm long. **Flowers** glandular-puberulent externally, calyx 4–8 mm long, 3–5 mm diam., lobes 2–4 mm long, triangular and acute; **corolla** 14–38(–60) mm long, 3.5–6(–10) mm diam., tubular, dark red to red-orange (pink or purple), upper lip 6–12 mm long, lower lobes ca. 2 mm long; functional stamens 2; thecae glabrous. **Fruits** 6–12 mm long, 4–7 mm diam., ovoid, dark; seeds 0.8–1.2 mm long, 0.4–0.6 mm thick, wedge shaped, with a deeply reticulated surface.

Plants of open sites in lower montane evergreen or partly deciduous formations, 1000–1800 m elevation (500–2800 m in Mexico). Flowering primarily in July–December in Costa Rica (flowering and fruiting throughout the year in Nicaragua). In Costa Rica this species has been collected only at the eastern and western edges of the Meseta Central and in the region between Paraiso and Orosí. This species ranges from northern Mexico to Panama.

Lamourouxia viscosa is recognized by its minute gland-tipped hairs on stems and flowers, stiff sessile opposite leaves that often surround the stem at their cordate bases, and lower montane habitats. This species is most closely related to the Mexican species *L. smithii* Pringle and *L. rhinanthifolia* Kunth in H.B.K. Costa Rican collections of *L. viscosa* do not possess leaves and flowers as large as some found in Mexico.

Leucocarpus D. Don in Sweet

Herbs, stems erect, quadrangular in cross-section and often with 4 longitudinal wings, glabrous or sparsely puberulent. **Leaves** opposite, sessile, narrow and serrulate, cordate-amplexicaul at the

base, venation pinnate, drying yellowish brown. **Inflorescences** cymose, solitary in distal leaf axils, peduncles with bracteoles subtending the pedicels or secondary inflorescence branches, bracteoles absent at the base of the calyx. **Flowers** with cupulate thin-walled calyx, 5-veined, persisting in fruit, calyx lobes narrow and tooth-like; **corolla** tubular or tubular-campanulate, somewhat bilaterally symmetrical with subequal upper and lower lips, glabrous externally, upper lip exterior in bud, 2-lobed, lower lip 3-lobed, puberulent at the mouth within; stamens 4 in 2 unequal pairs (or with only 2 fertile stamens), anthers with 2 slightly diverging thecae, staminodes rarely present; ovary conical, 2-locular, ovules many, style thickened at the apex, stigma 2-lobed. **Fruits** fleshy indehiscent berries, white, pericarp thin, style base forming a small beak; seeds immersed in pulp, minutely reticulate.

Leucocarpus is a monotypic genus, ranging from Mexico to Bolivia. It is included in the tribe Dodartieae, with *Hemichaena*, *Mimulus*, and *Mazus*. At one time, Bentham included *Hemichaena* in *Leucocarpus*, but the genera are now considered distinct.

Leucocarpus perfoliatus (Kunth in H.B.K.)

Benth. in DC., Prodr. 10: 335. 1846. *Mimulus perfoliatus* Kunth in H.B.K., Nov. Gen. Sp. 2: 371. 1817. *Conobea alata* Graham, Edinburgh New. Philos. J. 10: 168. 1830. *L. alatus* (Graham) D. Don in Sweet, Brit. Fl. Gard. 2: tab. 124. 1833. Figure 6.

Erect **herbs** or shrubs 0.5–2.5 m tall, flowering stems usually unbranched, leafy stems 3–8 mm wide, with 4 prominent longitudinal wings (ridges), wings 0.3–2 mm wide, usually glabrous. **Leaves** of the same node slightly united at the base to form a short interpetiolar ridge, sessile and amplexicaul; **leaf blades** 8–23(–28) cm long, 1–4.5(–6) cm wide, narrowly lanceolate to very narrowly elliptic-oblong, tapering gradually to the acute or acuminate apex, margin serrulate with 3–5 teeth/cm, cuneate in the lower ¼ but slightly expanded at the rounded-auriculate base, drying thin-chartaceous, usually glabrous, 2° veins 10–14/side. **Inflorescences** 2–6 cm long, axillary cymes or with 2° branching, with 2–12 flowers, peduncles 1–3 cm long, 0.7–1.3 mm diam., glabrous or minutely puberulent with thin hairs 0.1–0.2 mm long, bracts 3–8 mm long, lanceolate, pedicels 4–14 mm long, minutely puberulent. **Flowers** with calyx 5–9 mm long, 2.5–3.5 mm

diam., campanulate, with narrow acute lobes 1–3 mm long, sparsely minutely puberulent; **corolla** (12–)14–17(–23) mm long, tubular with slightly expanded lobes, yellow to white, marked with yellow and barbate within, tube 2–5 mm diam., lobes slightly unequal; filaments 5–10 mm long; style 5–7 mm long. **Fruits** globose, 7–10 mm diam., white, fleshy; seeds 0.4–0.5 mm long, 0.2–0.3 mm wide, ellipsoid-oblong, yellowish brown, reticulation minute (visible at 50×).

Plants of open moist to wet sites in lower montane evergreen forest formations, 800–2200 m elevation. Probably flowering and fruiting throughout the year, but with most Costa Rican collections made in December–January and April–June. The species ranges from Veracruz, Mexico, to the highlands of western Panama and Bolivia.

Leucocarpus perfoliatus is recognized by the unbranched flowering stems with winged margins, sessile leaves with auriculate bases clasping the stems, axillary inflorescences, always shorter than the leaves, smaller tubular yellow corollas, and baccate fruit. Superficially, these plants are similar to *Hemichaena fruticosa* (q.v.), but that species has larger flowers and dry dehiscent fruits.

Limosella Linnaeus

REFERENCE—H. Glück, *Limosella* studien. Beitrage zur Systematik, Morphologie, und Biologie der Gattung *Limosella*. Bot. Jahrb. Syst. 66: 490–563. 1934. A. Lourtieg, Étude sur *Limosella*. Comité National Français des Recherches Antarctiques: Biologie 1(10): 165–173. 1964.

Very small **herbs**, annual or perennial, growing in shallow water or on moist soil, caespitose or with short stolon-like stems rooting from the nodes, glabrous or puberulent. **Leaves** from the apex of the rootstock or fasciculate at the nodes, densely clustered, sessile or with poorly differentiated petioles, blades linear to obovate, entire, flat or cylindrical, drying brown or yellowish, glabrous, venation obscure or with a midvein. **Inflorescences** of 1 to several flowers from the leaf axils, glabrous, bracts absent, pedicels usually shorter than the leaves, bracteoles absent at the base of the calyx. **Flowers** very small, glabrous externally, calyx campanulate, usually thin-walled, equal to or slightly shorter than the corolla tube, lobes 5 (4) with the posterior lobe exterior; **corolla** funnellform to campanulate, white to bluish or pinkish, tube short, lobes 3–5, subequal and

imbricate in bud, equal to or shorter than the corolla tube; stamens 4 (2, 5), included, filaments simple, borne near the middle of the tube, filaments of lower stamens crossing over the filaments of upper stamens, anther thecae confluent (1-theous), not mucronate; ovary ovoid to ellipsoid, 2-locular near the base, style short, stigma capitate. **Fruits** capsules or indehiscent, usually bivalvate; seeds small, numerous, ovoid, striate and reticulate.

A genus of ca. 11 species distributed widely over temperate and tropical montane regions but most diverse in the Southern Hemisphere. The very small size of the plants, their small flowers, and their aquatic or moist habitats help distinguish the genus. The genus is classified in the tribe Gratiolaeae and is often placed in the subtribe Limosellinae.

Limosella acaulis Sesse & Mociño, Fl. Mex. ed. 2: 143. 1894. *L. americana* Glück, Notizbl. Bot. Gart. Berlin Dahlem 12: 75. 1934. *L. americana* f. *submersa* Glück, loc. cit. 75. 1934. *L. americana* f. *natans* Glück, loc. cit. 76. 1934. *L. americana* f. *terrestris* Glück, loc. cit. 1934. Figure 1.

Small **herbs** to 5 cm tall, stems to 6 cm long or little developed (and plants acaulescent), rooting at the nodes, glabrous. **Leaves** rosulate or fasciculate, sessile or with poorly differentiated petioles to 4 cm long, clasping the stem at their base, glabrous throughout; **leaf blades** 4–15 mm long (–11 cm when linear), 0.7–4 mm wide, linear to narrowly oblong to spatulate or oblanceolate, apex usually rounded, margins entire, gradually narrowed at the base, drying brown or yellowish, midvein usually visible only near the base. **Inflorescences** of 1–3 flowers in leaf axils (but difficult to see among the crowded leaf bases), pedicels 10–30 mm long, ca. 0.4 mm wide, glabrous. **Flowers** glabrous externally, calyx 1.5–2 mm long, lobes 5, 0.3–0.7 mm long, narrowly triangular to oblong, dark coloring sometimes present between the lobes distally; **corolla** ca. 4 mm long, campanulate or subrotate, slightly zygomorphic (bilaterally symmetric), white, tube ca. 2.5 mm long, ca. 1.3 mm diam., lobes 3–5, 1–1.5 mm long, rotate; stamens 4 in 2 opposing pairs. **Fruits** 1.5–4 mm long, 1–3 mm diam., ovoid-ellipsoid, glabrous; seeds 0.5–1 mm long, 0.2–0.5 mm wide, striate.

Rarely collected plants in shallow water or wet soils, found only above 3300 m elevation in Cen-

tral America. Probably flowering and fruiting throughout the year. Known in Costa Rica from a single collection made in the Valle de los Conejos on Chirripo Grande (3400 m) in February (*Weston 12360*). The species ranges disjunctly from Mexico to Venezuela and Bolivia.

Limosella acaulis is distinguished by its moist and very high altitude habitat, the small size of the plants, mostly fasciculate linear sedge-like leaves, and very small flowers with white corollas that have three to five lobes. When seen from above, the flowers may be reminiscent of *Houstonia* (Rubiaceae), with four corolla lobes held in a single horizontal plane. Species are variable and individual populations are often isolated, so local variation is common. Also, the plant's habit changes with water depth and length of immersion. When submersed, leaves develop to be longer and more linear than spatulate; flowers remain closed and are cleistogamous. The Costa Rican collection describes the plants as forming small mats in a creek bed. Lourtieg (1964, cited above) placed most taxa as synonyms of *L. australis* R. Br., but we follow the decisions of Louis Williams regarding the circumscription of this species (Fiediana, Bot. 34: 121, 1972).

Linaria Miller

REFERENCE—D. Sutton, A. Revision of the Tribe Antirrhineae. British Museum (Natural History) & Oxford Univ. Press, 1988.

Herbs or subshrubs, annual, biennial or peren-

nial, erect, branching, mostly from the base, glabrous or less often glandular-puberulent, drying grayish to dark brown. **Leaves** alternate, sometimes opposite or verticillate near the base, leaf blades usually sessile, entire, linear to reniform, pinnately veined. **Inflorescences** colorful racemes or spikes (rarely flowers solitary in leaf axils), alternate along the rachis, bracts usually small, bracteoles absent at base of calyx. **Flowers** usually glabrous, calyx campanulate, with 5 sepals or 5 calyx lobes, equal or subequal, imbricate in bud, persisting in fruit; **corolla** tubular and strongly bilabiate, tube with a backward-pointing abaxial spur, upper (adaxial) lip bilobed and exterior in bud, lower (abaxial) lip 3-lobed and with a prominent raised palate near the entrance to the tube; stamens 4 in 2 pairs, included, filaments attached near the base of the tube, anthers with 2 parallel or divergent thecae, a staminode sometimes present; ovary 2-locular, ovules many, style slender, stigma small, 2-lobed or capitate. **Fruits** thin-walled capsules, ovoid to globose, dehiscent loculicidally into 2 valves or forming distal pores; seeds ovoid to discoid or C-shaped, testa thin, smooth to rugose.

Linaria is a genus of ca. 100 species, native to north temperate regions and the Mediterranean area. They are often grown in gardens for their colorful and complex flowers or their foliage. The corollas with backward-pointing spur and strongly two-lipped lobes are distinctive. The genus is classified in the tribe Antirrhineae and is closely related to *Cymbalaria* (q.v.). Although not known to be naturalized in Costa Rica, the following two species are likely to be present.

Key to the Species of *Linaria*

- 1a. Flowers yellow, corollas 20–30 mm long; planted in gardens and rarely escaping . . . *L. vulgaris*
- 1b. Flowers blue to purple, corollas 5–15 (20) mm long; weedy plants of cooler climates *L. canadensis*

Linaria canadensis (L.) Dumort., Bot. Cult. 2: 96. 1802. *Antirrhinum canadensis* L., Sp. Pl. 618. 1753. *L. texana* Scheele, Linnæa 21: 761. 1848.

Herbs, annual or biennial, flowering stems erect from a basal rosette of leafy stems, 15–50 cm tall, branching from the base, leafy stems 0.5–2.5 mm diam., glabrous. **Leaves** opposite or whorled near the base, alternate on erect stems,

sessile; **leaf blades** of erect stems 5–20 mm long, 1–2 mm wide, linear, apex acute to bluntly acute, margin entire, base cuneate, venation obscure. **Inflorescences** racemes (or appearing spicate), usually making up the distal half of erect stems, glabrous, bracts ca. 2 mm long, pedicels 1–4 mm long. **Flowers** glabrous externally, calyx 2–3.5 mm long, sepals 5, 0.5–1 mm wide; **corolla** 5–15(–20) mm long, blue to purple, spur 2–9 mm long, tube strongly 2-lipped, the throat open,

white; stamens 2–3 mm long; ovary 1–2 mm long, ovoid, style 1–2 mm long. **Fruits** 2–3.5 mm long, subglobose to rounded oblong, with persisting style 0.5 mm long; seeds 0.3–0.5 mm long, angled, smooth.

Linaria canadensis, native from southern Canada to northern Mexico, is a weed of open sunny sandy sites in cooler temperate or montane tropical climates (ca. 2000 m elevation in Mexico). Although not yet recorded for Central America, it is naturalized in South America and is likely to become established in our area. The unbranched erect stems, linear leaves, slender racemes, and blue corolla with spur help to distinguish this species.

Linaria vulgaris Miller, Gard. Dict. ed. 8. 1768.
Antirrhinum linaria L., Sp. Pl. 616. 1753.

Erect perennial **herbs** 0.2–0.8 m tall, spreading by underground stems to form persisting clumps, erect stems usually unbranched, 1–3 mm diam., usually glabrous. **Leaves** alternate and numerous along the stem, glabrous, sessile; **leaf blades** 3–5 cm long, 1–6 mm wide, linear to linear-lanceolate, secondary veins obscure. **Inflorescences** spicate racemes with crowded flowers, bracts ca. 1 cm long, similar to the leaves, pedicels 1–4 mm long, pedicels and flower oriented upward at an acute angle to the stem. **Flowers** with glabrous calyx, sepals 2–3.5 mm long, narrowly ovate, acute; **corolla** 2–3 cm long, yellow with orange near the mouth, tube with a spur equaling the tube and lobes in length, mouth of the corolla strongly bilabiate, upper (adaxial) lip 8–12 mm long, lower (abaxial) lip 6–9 mm long, with a puberulent rounded palate. **Fruits** 5–10 mm long, glabrous; seeds ca. 2 mm long, discoid and winged.

Linaria vulgaris, a native of Eurasia, is occasionally grown in gardens for its unusual yellow flowers, but it is more likely to be seen as a weed in cooler climates of the world. It is recognized by its often linear alternate leaves and the unusual two-lipped yellow corolla with basal spur. This species has not been recorded as naturalized in Central America. These plants sometimes produce abnormal flowers that are radially symmetric (not two-lipped) and have five spurs or none. Linnaeus mistakenly erected the genus *Peloria* for such plants, and the word *peloria* is now used to describe abnormal radially symmetric forms of flowers that are normally strongly bilaterally symmetric (zygomorphic).

Lindernia Allioni

REFERENCES—D. Miranda, Flavonoid and morphological studies of *Lindernia* Allioni (Scrophulariaceae) in South America. Bot. J. Linn. Soc. 75: 47–67. 1977. D. Philcox, Revision of the Mallesian species of *Lindernia* All. (Scrophulariaceae). Kew Bull. 22: 1–72. 1968. T. Yamazaki, Revision of the Indo-Chinese species of *Lindernia* All. J. Fac. Sci. Univ. Tokyo, Bot. 13: 1–64. 1981.

Small annual **herbs**, terrestrial or semiaquatic, erect to prostrate or creeping and rooting at the nodes, stems simple or branched, glabrous or puberulent, usually 4-angled, drying yellowish or brown. **Leaves** opposite, simple, small, sessile or petiolate, blades entire or denticulate, base often truncated to cordate, often glandular-punctate, venation pinnate or 3–5-veined from the base. **Inflorescences** of solitary flowers in the axils of distal leaves, less often terminal or axillary racemes or umbel-like clusters, bracts and bracteoles absent, pedicels slender, usually longer than the calyx. **Flowers** small, calyx tubular with 5 short spreading lobes or deeply parted to the base with 5 sepals, the sepals or lobes subequal, glabrous or puberulent externally, tube with 5 longitudinal ridges (sometimes winged); **corolla** tubular to campanulate, longer than the calyx (equaling the calyx and not opening in cleistogamous flowers), blue to purple or white, bilabiate, upper lip usually shorter and erect, entire or 2-lobed, lower lip 3-lobed and spreading; stamens 4 or with 2 fertile and 2 staminodes present, filaments often inserted at 2 levels in the distal half of the tube, anterior filaments often with a distinct spur near the base, upper filaments often bent just near the apex, anthers free or united in pairs, 2-thecous, thecae often widely divergent and X-shaped; ovary glabrous, 2-locular, ovules many, style slender, stigmas 2-lobed. **Fruits** dry capsules, ovoid to ellipsoid, globose or cylindric, dehiscent septically and 2-valved, the placentae winged; seeds many, oblong-elliptic, smooth to reticulate or alveolate with prominent transverse or longitudinal raised ridges.

A genus of 50 to 70 species widespread in tropical and temperate areas throughout the world, with the majority of species in tropical parts of Africa, Asia, and Australia. The genus is classified in the tribe Gratiioleae and placed in subtribe Lindernieae with *Torenia*. It seems likely that *L. crustacea* is indigenous to Costa Rica and that the

other two species have been introduced. These plants are generally found in marshes, at the edges of standing water, or in moist depressions, in open sunny or partly shaded sites. The preference for

moist soils, the short slender stems, small opposite leaves, small bluish flowers, tubular bilabiate corollas, four or two fertile stamens, and appendaged anther filaments help distinguish the genus.

Key to the Species of *Lindernia*

- 1a. Flowers subsessile, pedicels < 3 mm long, flowers solitary in leaf axils; corollas white or yellowish to pale lilac; leafy stems usually with puberulent longitudinal ridges; fruits 6–10 mm long *L. diffusa*
- 1b. Flowers borne on pedicels 3–23 mm long (longer pedicels at distal nodes), flowers often in terminal cyme-like groupings; corollas bluish to lilac, rose, or white marked with yellow; leafy stems glabrous or puberulent; fruits 3–4 mm long 2
- 2a. Calyx 5-lobed, united ca. 50% to form a tube (but splitting after anthesis and appearing as separate sepals in fruit); fruits ovoid, seeds 0.4–0.5 mm long; leaves petiolate *L. crustacea*
- 2b. Calyx with 5 sepals united only at the base; fruits ellipsoid, seeds 0.3–0.4 mm long; leaves sessile *L. dubia*

Lindernia crustacea (L.) F. v. Muell., Syst. Census Aust. Pl. 1: 97. 1882. *Capraria crustacea* L., Mant. Pl. 1: 87. 1767. *Torenia crustacea* (L.) Cham. & Schldl., Linnaea 2: 570. 1827. *Vandelila crustacea* (L.) Benth., Scroph. In. 35: 1835. *Pyxidaria crustacea* (L.) Kuntze, Rev. Gen. Pl. 2: 464. 1891. Figure 2.

Prostrate or procumbent **herbs** to 15 cm tall, rarely rooting at distal nodes, leafy stems 0.2–1.3 mm diam., longitudinally ribbed, glabrous or with thin crooked hairs 0.1–1 mm long. **Leaves** opposite, petioles 1–7 mm long, 0.4–0.7 mm wide, glabrous or sparsely puberulent, leaf bases not united across the stem; **leaf blades** 6–16 mm long, 4–15 mm wide, ovate to ovate-rounded or ovate-triangular, apex obtuse or rounded, margin serrate with 4–6 teeth/cm, base truncate to rounded-subcordate, drying membranaceous and yellowish green, minutely punctate, glabrous or very sparsely puberulent beneath and along margin, 2° veins 3–5/side. **Inflorescences** solitary axillary flowers or terminal cymes, pedicels 4–18(–25) mm long, 0.1–0.2 mm diam., glabrous or with few thin hairs to 0.4 mm long. **Flowers** with calyx 2–4 mm long, 1–1.8 mm diam., lobes 0.7–1.5 mm long, triangular and acute, glabrous or very sparsely puberulent; **corolla** 4–7 mm long, blue to violet or blue-purple (white), tube ca. 5 mm long, 1–1.5 mm diam.; fertile stamens 4 in 2 pairs, anthers connivent; ovary glabrous. **Fruits** 3–4 mm long, 2–2.5 mm wide, rounded-ovoid, central column (placenta) to 2 mm wide with smooth lateral wings and central reticulated area; seeds 0.4–0.5

mm long, 0.3–0.4 mm diam., oblong, yellowish, obscurely reticulate.

Uncommon plants of moist open sunny or partly shaded sites in lowland evergreen forest formations, 0–300(–1000) m elevation. It is also found along stream edges in seasonally dry areas. Flowering and fruiting throughout the year. This species is a widespread weed, now found in tropical and warm-temperate climates throughout the world.

Lindernia crustacea is recognized by its small, mostly prostrate habit, mostly glabrous parts, small ovate-serrate leaves, small blue flowers on prominent slender pedicels, calyx lobes united for half their length, small rounded fruit, and unusual persisting placenta with smooth lateral wings. In addition, the lower pair of anthers is inserted on the lower corolla lip. The persisting and expanded calyx often splits along the thin intercostal areas to produce separate sepals, appearing very different from the calyx in anthesis.

Lindernia diffusa (L.) Wettst. in Engl. & Prantl, Natürlichen Pflanzenfam. 4, 3b: 79. 1891. *Vandelila diffusa* L., Mant. Pl. 1: 89. 1767. *Pyxidaria diffusa* (L.) Kuntze, Rev. Gen. Pl. 2: 464. 1891. Figure 2.

Prostrate or decumbent **herbs** 2–15 cm tall, sometimes forming small mats to 25 cm wide, often rooting at the nodes, leafy stems 0.4–1.3 mm diam., quadrangular with 4 puberulent longitudinal ribs, the thin whitish hairs 0.2–0.3 mm long. **Leaves** opposite, united at the base to form

an interpetiolar line or ridge, subsessile or with petioles to 4 mm long; **leaf blades** 6–25 mm long, 4–24 mm wide, ovate to broadly ovate or rhombic, apex obtuse to rounded, margin serrate with 6–10 teeth/cm, base broadly obtuse to rounded and truncate, minutely punctate, glabrous above, with minute (0.1–0.2 mm) hairs along the veins beneath, venation subpalmate with 2–3 2° veins/side. **Inflorescences** of solitary axillary flowers, usually 2/node, pedicels 1–3 mm long, ca. 0.3 mm diam., minutely puberulent. **Flowers** with calyx 4–7 mm long, 1–1.5 mm diam., lobes 2–4 mm long, linear-lanceolate, glabrous or minutely puberulent on the major veins and margins of lobes; **corolla** 6–9 mm long, white, yellowish, or pale lilac with yellow interior; fertile stamens 4; ovary glabrous, style ca. 3 mm long. **Fruits** 6–10 mm long (including the 1–2 mm beak), 2.3–4 mm diam., ellipsoid or narrowly ovoid-ellipsoid; seeds 0.5–0.6 mm long ca. 0.3 mm diam., oblong, with minute spines and a reticulate-pitted surface.

Plants of open sunny sites in evergreen forest formations, 10–1200 m elevation. Probably flowering and fruiting throughout the year. Probably originating in the Old World, this species is now widespread in warmer climates.

Lindernia diffusa is recognized by its small size, stems with usually four puberulent ridges, small subsessile serrate leaves with broad blades, solitary axillary flowers on very short pedicels, and white corollas marked with yellow.

Lindernia dubia (L.) Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 141. 1935. *Gratiola dubia* L., Sp. Pl. 17. 1753. *Capraria gratiolooides* L., Syst. Veg. ed. 10: 1117. 1759. *G. inaequalis* Walt., Fl. Carol. 61. 1788. *G. anagallidea* Michx., Fl. Bor. Am. 1: 6. 1803. *Ilysanthes gratiolooides* (L.) Benth. in DC., Prodr. 10: 419. 1846. *L. gratiolooides* (L.) Lloyd & Fouc., Fl. Oest Fr. ed. 4: 246. 1886. *L. inaequalis* (Walt.) Pennell, Torrey 19: 149. 1919. *I. dubia* (L.) Barnhart, Bull. Torrey Bot. Club. 26: 376. 1899. *L. anagallidea* (Michx.) Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 152. 1935. Figure 4.

Herbs, stems procumbent or erect, 5–30 cm tall, simple or much-branched, rooting mostly at the base, leafy stems 0.2–1 mm diam., usually with 4 longitudinal ridges, glabrous. **Leaves** opposite, sessile, free or united at the base and forming an interpetiolar line; **leaf blades** 4–14(–25) mm long, 3–8(–10) mm wide, narrowly ovate to

narrowly ovate-triangular or lanceolate, apex acute to obtuse, margin entire or with 2 or 3 teeth/side, base acute to somewhat rounded, drying membranaceous, glabrous, venation usually palmate with 3 major veins. **Inflorescences** of solitary axillary flowers or cymes subtended by leaf-like bracts, pedicels 3–23 mm long, ca. 0.2 mm diam., glabrous, distal pedicels much longer than those at lower nodes. **Flowers** with calyx deeply 5-parted, sepals 1.8–2.5 mm long, 0.3–0.4 mm wide, linear-oblong, becoming 3–5 mm long in fruit but remaining narrow; **corolla** 5–10 mm long, blue or white with purplish throat or lilac to rose; fertile stamens 2, staminodes 2 and bifid at the apex; ovary glabrous, style 3 mm long. **Fruits** 3–6 mm long, ca. 2 mm wide, narrowly ovoid-oblong to oblong-ellipsoid; seeds 0.3–0.4 mm long, 0.2–0.3 mm diam., oblong, with longitudinal rows of pits.

Plants of open wet sites and marshes in evergreen or seasonally deciduous areas, 5–1100 m elevation. Probably flowering primarily at the end of the rainy season (November–January). Rarely encountered in Costa Rica, this species ranges from southern Canada and the eastern United States to southern South America and the West Indies.

Lindernia dubia is recognized by its small stature, moist habitats, lack of pubescence, opposite sessile leaves, distal flowers on longer pedicels, white and blue two-lipped corollas, and separate sepals. There is considerable diversity of leaf form, with some plants having narrowly ovate leaves (var. *anagallidea* (Michx.) Cooper) and other plants with more elongate narrow leaves (var. *dubia*). Holmgren (*Flora of the Great Plains*, 1986, p. 769) found that *L. anagallidea* cannot be effectively separated from *L. dubia*. Likewise, in 1984 D. A. Qualls annotated many North American collections as *L. dubia*. We follow their decision to consider the two as elements of the same species. *Lindernia microcalyx* Pennell & Stehle is very similar but has corollas 9–14 mm long; it has been collected along the Caribbean shore of Guatemala and Honduras (determinations by D. A. Qualls, 1984).

Lophospermum D. Don

REFERENCES—W. Elisens, Monograph of the Maurandyinae (Scrophulariaceae—Antirrhineae). Syst. Bot. Monogr. 5: 1–97. 1985. D. Sutton, A Revision of the Tribe Antirrhineae. British Mu-

seum (Natural History) & Oxford Univ. Press. 1988.

Perennial **herbs** or climbers, stems often scandent or clambering, branches often arising from a woody base, sparsely puberulent to glandular-villose, drying grayish or greenish. **Leaves** alternate, petioles well developed and often bending to facilitate climbing; leaf blades deltoid to reniform, apex acute to mucronate, margins dentate to broadly crenate, venation palmate. **Inflorescences** of solitary flowers in axils of leaves, pedicels horizontal to ascending, bracts and bracteoles absent. **Flowers** large, calyx urceolate or campanulate and expanded, sepals free or united at the base, narrowly to broadly ovate, glandular puberulent, often enlarging in fruit; **corolla** tubular-campanulate, somewhat bilabiate and open-throated, reddish to violet or purple distally (whitish or pale near the base), 5-lobed, upper 2 lobes recurved, lower 3 lobes projecting forward; stamens 4, subequal or in 2 pairs, included, connective often expanded, a staminode usually present; ovary glabrous or glandular puberulent, 2-locular, ovules many, stigma recurved or straight, forked and divergent (rarely conical and lobed). **Fruits** dry capsules, ovoid to globose, symmetric or asymmetric, dehiscent irregularly or poricidal, bivalved; seeds rounded with a wing around the margin.

A genus of 6 or 20 species, depending on whether the Mexican genus *Rhodochiton* Zucc. is included (following Elisens, 1985) or excluded (following Sutton, 1988). Species range from north-central Mexico to Guatemala; a few species are planted as ornamental climbers. These plants are characterized by the scandent or clambering habit, alternate leaves, twining petioles, deltate to cordiform blades, large corollas, and round seeds with thin peripheral wing. The one species found in Costa Rica was formerly placed in the genus *Maurandya*; both are placed in the tribe Antirrhineae.

Lophospermum erubescens D. Don in Sweet, Brit. Fl. Gard. ser. 2, 1: tab. 68 and after tab. 75. 1830. *Maurandya erubescens* (D. Don) Gray, Proc. Am. Acad. Arts 7: 377. 1868. *Asarina erubescens* (D. Don) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 174. 1947. Figure 8.

Climbing **herbs**, leafy stems 1–4 mm diam., pubescent with thin straight or crooked multicellular hairs 0.3–0.8 mm long, some hairs with

gland tips. **Leaves** alternate, petioles 3–6 cm long, 0.6–1.2 mm diam., often bent or curving (sometimes helping to support the stem), pubescent; **leaf blades** 3–7(–15) cm long, 2–6.5(–15) cm wide, triangular to triangular-rhombic or sagittate, apex acute, margin prominently crenate-serrate with teeth 0.5–6 mm high and 1–8 mm wide, base cordate, with thin whitish hairs 0.3–0.5 mm long above and below, major veins 3 or 5. **Inflorescences** of solitary axillary flowers, pedicels 2–7(–11) cm long, 0.7–1.4 mm diam., puberulent, not bent or twining. **Flowers** puberulent externally, calyx 15–24 mm long, sepals subequal, 10–14 mm wide, broadly ovate; **corolla** 6–7 cm long, tubular-campanulate, bright pink to red distally, tube constricted above the base, whitish within and with yellow hairs in the throat, ca. 2 cm wide at the mouth, lobes 10–14 mm long, 12–16 mm wide, rounded distally. **Fruits** 15–20 mm long, subtended by persisting sepals, surface with thin multicellular hairs; seeds ca. 2.5 × 2.5 mm, wings lateral with a narrow notch at apex and truncated base, body of the seed ca. 1.5 × 0.8 mm, tuberculate.

Lophospermum erubescens is characterized by its vining habit, twisted petioles, triangular and coarsely dentate leaf blades, broad sepals, and large, tubular, slightly asymmetric pink corollas. This species is native to the oak forests of the Sierra Madre Oriental of Mexico and is now commonly grown in gardens as a climbing ornamental. It has been collected as an escape at Monteverde, where it was flowering in January and September at ca. 1400 m, and north of San Isidro del General at 1500 m elevation, where it was flowering in April. Compare *Maurandya barclaiana* and *M. scandens*.

Maurandya Ortega

REFERENCES—W. Elisens, Monograph of the Maurandyinae (Scrophulariaceae—Antirrhineae). Syst. Bot. Monogr. 5: 1–97. 1985. D. Sutton, A Revision of the Tribe Antirrhineae. British Museum (Natural History) & Oxford Univ. Press. 1988.

Scandent **herbs**, annual or perennial, with thin flexible stems from a fibrous base or taproot, glabrous. **Leaves** alternate, petioles long and often twisting to support the twining habit; leaf blades hastate to sagittate or rarely cordiform, margins usually entire, glabrous, venation palmate. **Inflo-**

rescences of solitary flowers in leaf axils, pedicels long, terete or winged near the base, glabrous or glandular-puberulent distally, bracts and bracteoles absent. **Flowers** with 5 sepals united only at the base, equal, lanceolate, imbricate near the base (urceolate), margins entire, glabrous or glandular-pubescent; **corolla** tubular and prominently 2-lipped, with open or closed throat, pink to red, violet, or blue, often whitish near the base, glabrous to glandular-puberulent externally, upper lip with 2 recurved lobes, lower lip with 3 recurved or projecting lobes, often closing the mouth with the well-developed palate; stamens 4 in 2 pairs, included, inserted near the base of the tube, filaments villous at the base; ovary 2-locular, locules subequal or unequal, glabrous or with glandular trichomes, ovules many, stigma conical and recurved. **Fruits** dry 2-valved capsules, ovoid to

globose, dehiscence irregular, irregular-transverse or poricidal; seeds rectangular with tuberculate-cristate surface (ovoid with a peripheral wing and minute tuberculate surface sculpturing in *M. wislizeni*), dark brown.

As revised by Elisens (1985, cited above), *Maurandya* is a genus of four species ranging from the southwestern United States to central Mexico. Sutton (1988, cited above) recognizes only two species in the genus, transferring two species found in the southwestern United States to splinter genera. The genus is closely related to *Lophospermum*, and they are placed in the tribe Antirrhineae. Two species are likely to be found as garden ornamentals in Central America, and one has recently been collected as an escape. These plants have also been placed in the genus *Asarina*.

Key to the Species of *Maurandya*

- 1a. Seeds with lateral wings; corolla to 6 cm long (see *Lophospermum erubescens*)
- 1b. Seeds without wings; corolla to 4 cm long 2
- 2a. Calyx covered with short gland-tipped hairs; corolla usually blue-violet *M. barclaiana*
- 2b. Calyx glabrous or with few gland-tipped hairs; corolla usually pink *M. scandens*

Maurandya barclaiana Lindley, Bot. Reg. 13, tab. 1108. 1827. Figure 8.

Vines with slender herbaceous climbing stems and twisting petioles, leafy stems 0.6–1 mm diam., glabrous or minutely papillate-puberulent at the nodes. **Leaves** alternate, petioles 12–32 mm long, 0.3–0.5 mm diam., glabrous, often coiling around objects for support; **leaf blades** 16–24(–35) mm long, 14–35 mm wide, triangular-hastate or sagittate, apex acute, usually with 2 basal lobes, glabrous, venation subpalmate with 3 (5) major veins from the base. **Inflorescences** of solitary flowers in leaf axils, pedicels 15–55 mm, ca. 0.5 mm diam., straight or curved, glabrous except near the calyx. **Flowers** with calyx 8–16 mm long, 2–3 mm wide at base, lobes triangular with long narrow apex, covered with gland-tipped hairs 0.3–0.5 mm long; **corolla** 2.5–4 cm long, ca. 15 mm wide, blue-violet, lobes 6–10 mm long, filaments ca. 18 and 14 mm long. **Fruits** 11–17 mm long, ovoid; seeds with angular projections.

Maurandya barclaiana is a vining ornamental often planted in tropical gardens. It is recognized by its colorful tubular two-lipped corollas, glandular-puberulent calyx, often sagittate leaves, and twisting petioles.

Maurandya scandens (Cav.) Pers., Syn. Pl. 2: 160. 1806. *Usteria scandens* Cav., Icon. 2: 15, tab. 116. 1793. *Maurandya semperflorens* Ortega, Nov. Pl. Descr. Dec. 21. 1797. *Reichardia scandens* (Cav.) Roth, Catal. bot. 2: 65. 1800. *Asarina scandens* (Cav.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 175. 1947. Figure 8.

Herbaceous climbers with slender twining stems, often with adventitious roots, leafy stems 0.5–2 mm diam., glabrous. **Leaves** alternate, petioles 8–35(–42) mm long, 0.4–0.8 mm diam., glabrous, often bent or twisted along their length; **leaf blades** 2–5(–6) cm long, 1–3.5(–4.5) cm wide, sagittate to hastate or triangular, apex acute, margin entire, base cordate and usually with prominent lateral lobes, drying membranaceous, glabrous or minutely papillate-puberulent near the petiole attachment, major veins 5 or 7, the 3 central veins reaching the middle of the blade. **Inflorescences** of solitary axillary flowers, pedicels 2–6(–8.5) cm long, 0.4–1 mm diam., slightly thickened near the base, glabrous. **Flowers** with calyx 9–15 mm long, sepals 2–4 mm wide near the base, lanceolate, glabrous (rarely sparsely glandular-puberulent); **corolla** to 4 cm long, tubular-

campanulate, pink to pale purple, tube 2–3 cm long, lobes 6–10 mm long, rounded; filaments 16 and 12 mm long, lower filaments shorter; ovary glabrous or with glandular hairs near apex. **Fruits** 9–12 mm long, ovoid to oblong, locules subequal; seeds with rounded projections.

Maurandya scandens, a native of central Mexico, is planted as an ornamental climber in Central America. The thin twining stems, lack of pubescence, often twisted petioles, sagittate-triangular leaves, solitary axillary flowers, and tubular two-lipped pinkish corollas make the plants distinctive.

Mazus Loureiro

Small annual **herbs**, diffusely branched from a basal rosette, stems with longitudinal ridges, pubescent or subglabrous. **Leaves** opposite and crowded near the base, alternate distally, petioles poorly differentiated; **leaf blades** obovate with crenulate or coarsely dentate margins, venation pinnate. **Inflorescences** terminal racemes, flowers alternate and solitary along the rachis (often on 1 side), bracts minute or absent, pedicels well developed, lacking bracteoles. **Flowers** with campanulate or tubular calyx, 5-lobed, tube usually equaling the lobes in length, lobes equal in size and shape, glabrous or puberulent, slightly expanded and enclosing the fruit; **corolla** 2-lipped, light blue to white or lavender, tube short, upper lip 2-lobed, lower lip 3-lobed, larger than the upper and spreading; stamens 4 in 2 pairs, filaments inserted at the base of the tube, anthers divaricate, thecae contiguous, a staminode absent; ovary 2-locular, ovules many, style longer than the ovary, stigma broadly bilabiate. **Fruits** capsules, globose or slightly compressed, loculicidal, producing 2 entire valves; seeds, ovoid to oblong or angled, rugulose or reticulate, black.

Mazus is an Asian-Australian genus of 30 to 40 species that is placed in the tribe Dodartieae with *Mimulus* and *Leucocarpus*. The following species is now an occasional weed in temperate and tropical montane climates.

Mazus pumilus (Burm.f.) Steenis, *Nova Guinea* N.S. 9: 31. 1958. *Lobelia pumila* Burm.f., *Fl. Ind.* 186, t. 60, f. 3. 1768. *M. japonicus* (Thunb.) Kuntze, *Rev. Gen. Pl.* 1: 462. 1891. *Lindernia japonica* Thunb., *Fl. Jap.* 253. 1784. *M. rugosus* Lour., *Fl. Cochinch.* 385. 1790.

Annual **herbs** 3–15 cm tall, ascending or decumbent, sometimes forming small mats, stems to 20 cm long, leafy stems 0.8–1.5 mm diam., sparsely puberulent with hairs to 0.5 mm long. **Leaves** rosulate or crowded at the base, opposite leaf bases united across the stem, distal leaves smaller and alternate, petioles 2–15 mm long, with lateral margins not clearly differentiated from the blades; **leaf blades** 6–60 mm long, 4–20 mm wide, obovate to cuneate-oblong or oblanceolate, apex obtuse or rounded, margins of larger leaves with prominent lobes 0.5–3 mm long (separated by wide sinuses), base cuneate and decurrent, sparsely puberulent with hairs to 0.4 mm long, 2° veins 2 or 3/side. **Inflorescences** 3–8 cm long, racemes with 3–13 flowers separated by internodes to 12 mm long, bracts 1–2 mm long, linear-filiform, pedicels 2–6(–11) mm long, sparsely to densely papillate puberulent. **Flowers** with calyx 4–7 mm long, with 5 prominent veins, tube 1–2 mm diam., lobes 2–3 mm long, narrowly triangular or oblong, with 5 prominent longitudinal veins, glabrous or minutely papillate puberulent; **corolla** 7–10 mm long, pale violet and white, tubular, upper lobes erect, lower lip ca. 2 mm long with 2 raised longitudinal ridges adaxially, palate yellow or whitish; stamens included; stigma lobes closing after pollination. **Fruits** 2–4 mm long, 2–3 mm diam., obovoid and bisulcate, surface glabrous, smooth, enclosed within the persisting calyx cup; seeds oblong, minutely reticulate.

Mazus pumilus, native to eastern Asia, is rarely collected in the Neotropics. It is often found as a weed in gardens and open places (1000–2000 m). The species is recognized by its small size, narrowly obovate opposite leaves with crenulate margins and long-decurrent blades, few-flowered racemes with long pedicels, partly united calyx, and blue or pink two-lipped corolla. These plants may resemble species of *Veronica*, but that genus lacks the strongly two-lipped flowers and four stamens.

Mecardonia Ruiz & Pavón

REFERENCE—F. Pennell, Reconsideration of the *Bacopa–Herpestis* problem. *Proc. Acad. Nat. Sci. Philadelphia* 98: 83–98. 1946. R. Rossow, Revisión del género *Mecardonia* (Scrophulariaceae). *Candollea* 42: 431–474. 1987.

Erect or prostrate **herbs**, annual or perennial, stems with few to many branches, mostly glabrous, drying brown or blackish. **Leaves** opposite,

sessile or short-petiolate, blades with serrate margins, usually glabrous, glandular-punctate, venation pinnate with most veins diverging in the proximal half of the blade. **Inflorescences** of solitary axillary flowers (2/node), 2 small linear bracts subtending the pedicel, bracteoles absent at the base of the calyx, pedicels slender. **Flowers** with deeply 5-parted calyx, sepals unequal in width with 3 broad outer ones; **corolla** tubular-campanulate, slightly 2-lipped and sometimes with a prominent palate (personate), yellow or white, upper lip slightly 2-lobed, lower lip 3-lobed; stamens 4 in 2 pairs, inserted near the base of the tube, thecae stipitate on short arms of the connective, a short staminode sometimes present; ovary 2-locular, ovules many, stigma flattened, 2-lobed, slightly bent. **Fruits** thin-walled capsules, dehiscence loculicidal; seeds oblong, surface reticulate and ridged.

A tropical and warm-temperate American genus of ca. 15 species, the majority in South American. The species have sometimes been united with those of *Bacopa*, but Pennell (1946) separated them because of the stipitate anther-thecae and the yellow pigmentation of the corolla. The anthers, the gland-dotted foliage, the slightly bilobed deflexed stigma, and the loculicidal capsule strengthen the distinction and indicate a close relationship with *Stemodia*. In Costa Rica, *Mecardonia* differs from *Stemodia* in having yellow corollas and pedicels with small bracts at the base. However, these distinctions do not hold over the entire range of all species, and it may be necessary to reevaluate the genera.

Mecardonia procumbens (Mill.) Small, Fl. S.E. U.S. 1065 & 1338. 1903. *Erinus procumbens* Mill., Gard. Dict. ed. 8. 1768. *Lindernia dianthera* Sw., Prodr. 92. 1788. *Herpestis caparioides* Kunth in H.B.K., Nov. Gen. Sp. 2: 368. 1818. *H. peduncularis* Benth., Bot. Mag. 2: 56. 1836. *Bacopa procumbens* (Mill.) Greenman, Publ. Field Columb. Mus. Bot. Ser. 2: 261. 1907. Figure 2.

Herbs, prostrate to procumbent, stems to 40 cm long, distal stems few-branched, sometimes rooting at the proximal nodes, leafy stems 0.4–2 mm diam., glabrous, with 4 longitudinal ridges. **Leaves** opposite, sessile or with poorly defined petioles to 4 mm long; **leaf blades** 6–24 mm long, 4–16 mm wide, ovate-elliptic to broadly or narrowly elliptic, apex obtuse, margin with 6–9 teeth/cm, base obtuse to cuneate, drying charta-

ceous and often blackish, glabrous, 2° veins 2 or 3/side. **Inflorescences** of solitary axillary flowers, linear bracts ca. 2 mm long at base of pedicel, pedicels 2–16(–24) mm long, 0.2–0.4 mm diam., glabrous. **Flowers** glabrous externally, calyx 5–9 mm long, outer 3 sepals 2.7–4 mm wide, ovate to lanceolate; **corolla** 8–10 mm long, tube ca. 7 mm long, yellow, purplish in the throat, barbate in the mouth, lobes 1–2 mm long; stamens 4, filaments borne on the lower half of the tube, a staminode sometimes present. **Fruits** 4–6 mm long, ovoid, dehiscent from the apex, placenta spongy; seeds 0.4–0.5 mm long, ca. 0.2 mm diam., oblong or ovoid, minutely reticulate, light brown.

Plants of open sunny or partly shaded sites on wet soils or wet sand in evergreen or deciduous areas, 0–1200(–2400) m elevation. Flowering and fruiting throughout the year. The species is particularly common in areas supporting evergreen lowland rain forest formations. The species ranges from Mexico to Uruguay and Argentina.

Mecardonia procumbens is recognized by its short herbaceous stems, general lack of pubescence, subsessile opposite serrate leaves, solitary axillary flowers on prominent pedicels, calyx with wide outer sepals and narrow inner sepals, and yellow tubular two-lipped corolla. These plants resemble species of *Bacopa*, *Lindernia*, and *Stemodia*, both in growth habit and in preference for moist open sites. This species can be separated from those in the other genera by the bright yellow corolla, glabrous gland-dotted foliage and bracteolate pedicels. This species is very closely related to *M. montevidensis* (Spreng.) Kuntze of southern South America.

Micranthemum Michaux

REFERENCE—L. O. Williams, Tropical American plants XII. Fieldiana, Bot. 34: 101–132. 1972 (*Micranthemum* pp. 122–124).

Small slender stemmed **herbs**, aquatic or growing in wet places, diffuse and much-branched, nodes often with adventitious roots. **Leaves** opposite, sessile, small, blades with entire margins, thin, usually glabrous, venation palmate. **Inflorescences** of solitary (rarely 2) axillary flowers, usually with 1 flower/node, bracts and bracteoles absent, pedicels short. **Flowers** minute, calyx with 4 or 5 lobes or 4 or 5 sepals, lobes equal, tube short or absent, glabrous or sparsely puberulent; **corolla** 2-lipped, tube very short, adaxial lip short

and 2-lobed, abaxial lip prominent and 3-lobed; stamens 2, filaments inserted at the mouth of the tube abaxially, anthers 2-theous, staminodes absent; ovary 1- or 2-locular, ovules many, style short, stigma 2-lobed. **Fruits** dry capsules, globose or ovoid, splitting irregularly; seeds oblong, with longitudinal ridges.

Micranthemum is a genus of perhaps 10 to 12 species, ranging from the southeastern United States to southern South America. It is most diverse in Cuba. The genus is recognized by its small slender-stemmed aquatic or semiaquatic habit, small sessile rounded leaves, minute solitary flowers, and small two-lipped corolla with two distal stamens. These delicate little plants are sometimes grown in freshwater aquaria. Although rarely collected in Central America, it is represented by the following species in Costa Rica.

Micranthemum umbrosum (J. F. Gmelin) Blake, *Rhodora* 17: 131. 1915. *Anonymous umbrosa* Walter, *Fl. Carol.* 63. 1788. *Globifera umbrosum* (Walter) J. F. Gmelin, *Syst. Nat.* 32. 1791. Figure 1.

Herbs, aquatic or in wet sites, creeping or often forming small mats, stems to ca. 12 cm long, leafy stems 0.2–0.8 mm diam., glabrous, with 2 longitudinal ridges. **Leaves** sessile, base of opposing leaves often forming a line or ridge across the stem; **leaf blades** 3–8 mm long, 2–7 mm wide, ovate-orbicular to rounded-obovate, apex obtuse to rounded, margins entire, obtuse or rounded at the contracted base, drying greenish and translucent, glabrous, with 3 major veins and 2 lateral veins. **Inflorescences** of solitary axillary flowers, usually with 1 flower/node, pedicels 0.5–1 mm long, 0.2–0.4 mm diam., glabrous. **Flowers** with calyx 0.8–1.3 mm long, sepals 4, equal and separate nearly to the base, narrowly oblong, with few minute hairs or glabrous; **corolla** ca. 1.5 mm long, white, tube very short; stamens 2, attached at the base of the abaxial sinuses. **Fruits** ca. 1 mm diam., globose, thin-walled, 1-locular; seeds 0.3–0.4 mm long, ca. 0.2 mm diam., oblong, yellowish, with minutely ribbed longitudinal ridges (50×).

Micranthemum umbrosum, ranging from the southeastern United States to South America, is rarely collected in Central America, but the very small size of the plants and their aquatic or wet habitats may have resulted in the species being overlooked. The species has been collected in Honduras, Nicaragua, and the Tortuguero region of northeastern Costa Rica. The slender glabrous

stems, small opposite sessile rounded leaves, minute solitary flowers, white two-lipped corolla with two stamens, and thin-walled capsules with one locule help distinguish these plants. *Micranthemum standleyi* Williams, an endemic of Guatemala, has smaller flowers, ovoid fruits, and pilose calyx lobes. *Micranthemum pilosum* Ernst, from Venezuela, is also similar, but it is possible that these are only variants of *M. umbrosum* in a broad sense.

Mimulus Linnaeus

REFERENCE—A. Grant, A monograph of the genus *Mimulus*. *Ann. Missouri Bot. Gard.* 11: 98–388. 1924.

Annual or perennial **herbs** (rarely shrubs), often preferring moist sites, decumbent or erect, with viscid pubescence or glabrous. **Leaves** opposite, simple, sessile or petiolate, blades entire or dentate, venation pinnate or palmate. **Inflorescences** of solitary flowers in leaf axils or forming terminal racemes, bracts absent or leaf-like, pedicels without bracteoles at the apex. **Flowers** showy, calyx tubular to campanulate, almost as long as the corolla, with 5 prominent veins, tube longer than the 5 short lobes or teeth, lobes usually unequal; **corolla** tubular or narrowly campanulate, 2-lipped, lips shorter than the tube, adaxial lip 2-lobed, abaxial lip 3-lobed, lobes subequal, usually with 2 yellowish protuberances in the throat; stamens 4 in 2 unequal pairs, included or exerted, filaments attached near the base of the tube, linear, anthers 2-theous with the thecae divaricate and confluent at the apex; ovary 2-locular, ovules many, style included, stigma flattened and 2-lobed. **Fruits** capsules, oblong to linear, thin- or thick-walled, dehiscence loculicidal, enclosed within the persisting and enlarged calyx tube; seeds small, smooth or reticulate.

Mimulus is a genus of ca. 150 species ranging from the Americas to Africa and Asia but with most of the species in western North America. Colorful species (monkey flowers) are grown in temperate gardens. No specimens of this genus have been collected in Costa Rica, but the following species may occur.

Mimulus glabratus Kunth in H.B.K., *Nov. Gen. Sp.* 2: ed. quarto 370. 1818. Figure 1.

Perennial **herbs**, procumbent or prostrate, 4–40 cm long, rooting at many lower nodes, leafy stems

0.3–4 mm diam. (dried), succulent in life, glabrous, nodes with an interpetiolar line formed by the clasping leaf bases, rooting at lower nodes. **Leaves** opposite, subsessile near the apex of stems or with petioles 2–18 mm long, 0.4–2 mm wide, with lateral margins continuous with the blade margins; **leaf blades** 8–45 mm long, 4–35 mm wide, ovate to ovate-oblong or ovate-orbicular, apex obtuse to rounded, margins with 3–5 prominent teeth/cm, base obtuse or truncated, drying grayish green, glabrous, venation palmate with 3–5 major veins. **Inflorescences** of solitary flowers axillary to foliage leaves (2/node), pedicels 12–42 mm long, 0.4–0.8 mm diam., glabrous. **Flowers** with calyx 5–10 mm long (14 mm in fruit), 2.5–4 mm diam., tubular, upper lobe larger (ca. 4 mm) than lower lobes (ca. 2 mm), glabrous; **corolla** 7–18 mm long, yellow with red spots within the throat, tube 2.5–4 mm diam., lobes 1–2 mm long. **Fruits** 6–10 mm long, 5–6 mm diam., included within the calyx tube; seeds 0.4–0.5 mm long, ca. 0.3 mm diam., oblong, brown, with poorly defined longitudinal ridges.

Mimulus glabratus ranges from the southern United States and Mexico to Nicaragua and from Colombia to Chile. In tropical environments it grows in wet sites at 100–2200 m elevation. These plants are recognized by their wet habitat, creeping stems with adventitious roots, lack of pubescence, opposite petiolate leaves, solitary axillary flowers on slender pedicels, tubular-plicate calyx with unequal lobes, and yellow two-lipped corolla with short lobes. Although not collected between Nicaragua and Colombia, this species may occur in our area.

Penstemon Mitchell

REFERENCE—R. Straw, The penstemons of Mexico. II. *Penstemon hartwegii*, *Penstemon gentianoides*, and their allies. Bol. Soc. Bot. Mexico 27: 1–25. 1962.

Perennial **herbs** or subshrubs, mostly erect, stems simple or branching from near the base, glabrous or pubescent. **Leaves** opposite, the lower leaves often petiolate, distal leaves often sessile and clasping the stem or bract-like; leaf blades serrate or entire, acute to rounded, venation pinnate. **Inflorescences** terminal panicles or thyrses (often racemiform), the partial inflorescences usually cymose, pedunculate with dichotomous branching, subtended by leaf-like or small bracts,

glabrous or puberulent, bracteoles present or absent. **Flowers** small or large, calyx deeply 5-parted, sepals imbricate in bud, equal or subequal; **corolla** tubular to tubular-campanulate, often narrowed at the base and abruptly expanded, 2-lipped, mostly blue to purple, sometimes red or white, upper (adaxial) lip 2-lobed and often erect, lower (abaxial) lip spreading or reflexed and 3-lobed; stamens 4 in 2 pairs, shorter than the corolla, bases glandular and nectariferous, filaments attached near the base of the tube, anthers glabrous or villous, thecae distinct or confluent, a staminode present and conspicuous; ovary ovoid, 2-locular, ovules many, style slender, stigma slightly 2-lobed or subcapitate. **Fruits** dry capsules, ovoid to globose, dehiscence septicidal and often loculicidal, valves entire or bifid; seeds many, dark, angular, rugulose to smooth, rarely winged along the margins.

Penstemon is one of the largest genera of Scrophulariaceae, with ca. 300 species ranging from temperate North America into the mountains of Mexico and Guatemala. The greatest number of species are found in the mountains of the western United States. The genus is identified by the tubular to campanulate flowers with a conspicuous staminode oriented on the lower (abaxial) side of the tube. Several species are colorful ornamentals, grown widely in temperate or tropical montane gardens. The following species is likely to be seen in Costa Rican gardens.

Penstemon gentianoides (Kunth in H.B.K.) Poir-et, Dict. Sci. Nat. 38: 385. 1825. *Chelone gentianoides* Kunth in H.B.K., Nov. Gen. Sp. 2: 363. tab. 172. 1818. *P. skutchii* Straw, Bol. Soc. Bot. Mexico 27: 13. 1962. Figure 8.

Erect perennial **herbs** or subshrubs 0.6–1.5 m tall, branched mostly in the lower half, leafy stems 2–6 mm diam., terete, glabrous or with thin straight hairs 0.1–0.2 mm long, nodes with interpetiolar ridges. **Leaves** opposite (but often with axillary short-shoots and giving a verticillate appearance), sessile or subsessile; **leaf blades** 4–12 cm long, 5–20 mm wide, lanceolate to linear-lanceolate, apex acute, margin entire, base cuneate to rounded, drying stiffly chartaceous, usually glabrous (except at the base), punctate above and below, 2° veins often obscure. **Inflorescences** 10–35 cm long, racemiform thyrses with axillary groups of (1–)3–9 flowers, bracts (reduced leaves) 12–30 mm long, usually lanceolate, peduncles 4–12 mm long, often terminated by opposite brac-

teoles 3–8 mm long, pedicels 3–12 mm long, minutely puberulent or subglabrous. **Flowers** with calyx 6–10 mm long, sepals 3–5 mm wide, broadly imbricate, glabrous or puberulent; **corolla** 2.5–4 cm long, tube 7–10 mm diam., narrowed near the base, deep purple to rose, red, or white, glabrous or minutely puberulent, lobes 6–10 mm long, throat white; filaments glabrous, anthers included, staminode ca. 22 mm long; ovary 5–7 mm long. **Fruits** 8–12 mm long, 5–6 mm wide, ovoid, style base persisting, septicial and loculicidal; seeds black, angular, rugulose.

Penstemon gentianoides, native to the higher (2400–4000 m) mountains of Mexico and Guatemala, is sometimes cultivated in gardens of the Meseta Central and at higher elevations. The spicate or racemiform arrangement of verticillate groups of large colorful flowers, with tubular corollas slightly expanded above the base, and the prominent staminode help to distinguish these plants.

Russelia Jacquin

REFERENCE—M. Carlson, Monograph of the genus *Russelia*. Fieldiana, Bot. 29: 231–292. 1957.

Perennial **shrubs** or herbaceous subshrubs from a woody base, erect or with pendent or scandent stems, distal branches few to many, stems angular or terete, puberulent or glabrous. **Leaves** opposite or whorled (caducous in *R. equisetiformis*), sub-

sessile or short-petiolate, blades usually ovate to lanceolate, margin entire or dentate to deeply incised, glandular (resinous) peltate scales (dots) often present, venation pinnate. **Inflorescences** dichotomous cymes, 1–3 in leaf axils or subtended by reduced bract-like leaves, often verticillate, subsessile to long pedunculate, linear bracts subtending the slender pedicels, bracteoles absent at the base of the calyx. **Flowers** mostly small (1–2 cm), calyx deeply 5-lobed or with 5 sepals, ovate to lanceolate, imbricate in bud, with or without peltate glands; **corolla** tubular to funnelliform, slightly 2-lipped, red to pink (white), the 5 lobes slightly unequal, the 2 (upper) adaxial lobes outside in bud, lower lip 3-lobed; stamens 4 in 2 unequal pairs, included, filaments borne in the lower half of the tube, thecae divaricate and confluent, a short staminode usually present; ovary 2-locular, ovules many, style slender, stigma slightly thickened. **Fruits** dry capsules, ovoid to subglobose, glabrous, dehiscence septicial (secondarily loculicidal); seeds small, slightly rugulose, developing among translucent fragmenting hairs (claters) produced by the placenta.

Russelia is a genus of 51 species centered in Mexico and Guatemala, with one species reaching Cuba and Colombia. The genus has been placed in its own tribe because of the unusual hair-like fragments in the capsule. The small tubular red flowers (only slightly two-lipped) in axillary cymes and the peltate glands (when present) also help to distinguish members of this genus. Two species are found in Costa Rica.

Key to the Species of *Russelia*

- 1a. Common wild plants of seasonally dry habitats; leaves ovate, subsessile, 1–9 cm long; stems with opposite branches; inflorescences > 2-flowered; corollas 10–16 mm long *R. sarmentosa*
- 1b. Plants grown in gardens; leaves falling off early and stems and verticillate branches leafless; inflorescences 2-flowered; corollas 15–30 mm long *R. equisetiformis*

Russelia equisetiformis Schldl. & Cham., Linnaea 6: 377. 1831. *R. juncea* Zucc., Flora 15, Beibl. 2: 99. 1832.

Erect **subshrubs** to 1 m tall, much-branched, lower nodes with whorls of 4–8 branches, distal nodes with 2 branches or peduncles at each node, longitudinal ridges 2, 4, or 6, distal stems usually leafless, 0.7–6 mm diam., glabrous or minutely puberulent near the nodes with thin hairs 0.1–0.3 mm long. **Leaves** opposite or verticillate, usually

caducous, and absent at distal stems, petioles 3–4 mm long and often remaining appressed to the stems when blades fall; lower larger leaf blades 8–15 mm long, 6–9 mm wide, ovate to elliptic. **Inflorescences** 2–16 cm long, often resembling open racemose panicles, usually with 2–4 peduncles/node, each peduncle with 1 or 2 flowers, basal peduncles 0.5–1.5 mm diam., glabrous, with 2 or 4 prominent longitudinal ridges, bracteoles 1–2 mm long, linear, pedicels 6–15 mm long, 0.2–0.3 mm diam. **Flowers** glabrous externally, calyx

2–3 mm long, imbricate, acute or acuminate, glabrous; corolla 15–30 mm long, 2–4 mm diam., tubular-funnelform, bright red, glabrous within; stamens 18 and 20 mm long, anthers near mouth of the tube, staminode present; ovary 2 mm long, ovoid, style 15 mm long, stigma minute. **Fruits** 3–6 mm diam., globose; seeds light brown, among white hairs within the capsule.

Russelia equisetiformis is a popular garden plant because of its slender green leafless stems and bright red flowers. It is distinctive because of the ridged stems and verticillate arching branches, which resemble those of *Equisetum*. Common names in Central America are *coral* and *lluvia de coral*. The species is native to Mexico and is an occasional roadside escape in the Meseta Central.

Russelia sarmentosa Jacq., Enum. Pl. Syst. 6: 25. 1760. *R. colombiana* Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 186. 1920. *R. flavoviridis* Blake, Contrib. U.S. Natl. Herb. 24: 22. 1922. *R. tabacensis* Lundell, Contrib. Univ. Michigan Herb. 6: 59. 1941. *R. oxyphylla* Lundell, loc. cit. 7: 51. 1942. Figure 5.

Herbs or weak-stemmed **shrubs** 0.5–2 m tall, erect or spreading, base woody, distal flowering stems usually unbranched, leafy stems 1–5 mm diam., strongly 4- or 6-angled with raised longitudinal ridges, puberulent with thin whitish hairs 0.1–0.3 mm long or glabrous (except at the nodes). **Leaves** 2 or 3 at each node, subsessile with petioles 0.5–4 mm long, often forming an interpetiolar line across the stem, lateral margins puberulent; **leaf blades** 1–7(–9) cm long, 1–5(–6) cm wide, ovate to broadly ovate or ovate-triangular, apex acute, margin with 2–5 teeth/cm, teeth 0.5–2 mm long, obtuse or truncated at the base, drying dark or grayish, glabrous or puberulent above, usually more pubescent beneath with hairs 0.2–0.4 mm long, peltate glands (ca. 0.2 mm diam.) often present on both surfaces, 2° veins 3–5/side and strongly ascending. **Inflorescences** 2–3 cm long, congested verticels of cymes in distal leaf axils, 12–20 flowers/cyme, peduncles 2–18 mm long, resembling the stems, bracts 3–4 mm long, linear, pedicels 5–8 mm long. **Flowers** with calyx 3–4 mm long, ca. 1.3 mm diam., lobes 2–3 mm long, with thin lateral margins and acuminate apex, often with peltate glands; **corolla** 10–14(–16) mm long, 1.5–3 mm diam., tubular, deep red, puberulent within, lobes subequal, 1.3–3 mm long; stamens ca. 8 and 6 mm long, inserted near the middle of the tube, anthers white; ovary 1–2

mm long, style 4–8 mm long. **Fruits** 4–5 mm long (not including the 0.5–4 mm style base), 4–5 mm diam., rounded-ovoid to subglobose, drying dark; seeds 0.4–0.5 mm long, ca. 0.2 mm wide, dark, among yellowish hairs.

Common plants of open weedy sites and forest edges in deciduous and partly deciduous (rarely evergreen) forest formations, 0–1300 m elevation. Flowering and fruiting throughout the year but collected most often in July–August and December–January. The species ranges from Mexico to Cuba and Colombia.

Russelia sarmentosa is recognized by the often shrub-like habit, stiff few-branched distal stems with two or three subsessile leaves at each node, short cymes often forming compact verticels of flowers and fruits, and bright red tubular corollas. The prominent longitudinal ridges on stems, peltate glands on leaf surfaces and calyx (when present), and sepals broadly overlapping at the base are also helpful in recognizing this common species. We agree with Margery Carlson's delimitation (1957, cited above) of this wide-ranging and variable species, but we do not believe that the recognition of forms and varieties is useful. The common name is *coralillo*.

Schistophragma Bentham ex Endlicher

Small annual **herbs**, erect or procumbent, stems quadrangular and with longitudinal ridges, glabrous or sparsely minutely puberulent, drying yellowish brown. **Leaves** opposite, petiolate, blades deeply pinnatisect with few opposite or alternate narrow lobes (smaller leaves sometimes linear-oblancoleate), margins entire or with a few distal teeth, venation pinnate. **Inflorescences** of solitary flowers axillary to distal leaves, bracts and bracteoles absent, pedicels slender. **Flowers** small, calyx divided to near the base, sepals or calyx lobes 5, narrow, acute, subequal; **corolla** tubular and slightly 2-lipped, upper (adaxial) lip with 1 emarginate lobe, lower (abaxial) lip 3-lobed; stamens 4, in 2 subequal pairs, included; ovary narrowly ellipsoid, 2-locular, ovules many, style slender, dilated at apex. **Fruits** linear capsules, somewhat compressed and bisulcate, septical; seeds oblong, surface with compressed spiral ridges.

The delimitation of *Schistophragma* and its distinction from *Leucospora* Nuttall and *Cono-bea* Aubl. is the subject of disagreement. B. L. Turner (Turner & Cowan, Phytologia 74: 61–103, 1993) recognizes three species of *Schistophragma* and

includes *Leucospora* within *Stemodia*. D. Keil (pers. comm.) includes the species of *Schistophragma* in his concept of *Leucospora*, which he retains as distinct from *Stemodia*. *Schistophragma* is placed in the tribe Gratioloae, subtribe Stemodiinae. The spirally striate seeds are very unusual in the Scrophulariaceae, but seeds of this type are sometimes found in the Gesneriaceae. The small size of the plants, narrow or pinnatisect leaves, small tubular flowers, and very narrow capsules make these plants distinctive. The linear fruits resemble those of some Brassicaceae. Among American Scrophulariaceae, only *Mabrya* Elisens, from Mexico, has similar linear fruits.

Schistophragma mexicana Benth. ex D. Dietr., Syn. Pl. 3: 513. 1842. *S. pusilla* Benth. in DC., Prodr. 10: 392. 1846. *Conobea pusilla* (Benth.) Benth. & Hook. ex Jackson, Index Kew 1, fasc. 1: 596. 1893. *Stemodia siligiosa* Sessé & Moçino, Pl. Nov. Hisp. ed. 1: 98. 1887–1890, ed. 2: 91. 1893. Figure 4.

Erect to decumbent annual **herbs** 6–25 cm tall, with few or many branches, leafy stems 0.3–1 mm diam., with 4 longitudinal ridges (quadrangular in cross-section), glabrous or with few minute hairs, nodes lacking interpetiolar lines. **Leaves** opposite, deeply pinnatifid, petioles 2–7 mm long (to first lobe), undifferentiated from the narrow rachis, 0.2–0.5 mm wide, sulcate adaxially; **leaf blades** 4–18 mm long, to 12 mm wide, deeply pinnatisect with 3–7 narrow lobes (including the distal extension of the rachis), lobes 0.3–2 mm wide, entire or the larger with 1 or 2 lateral teeth, glabrous or minutely puberulent on the veins beneath, proximal lobes rarely with 1 or 2 2° lobes (bipinnatifid). **Inflorescences** of solitary axillary flowers, usually 2/ node, pedicels 3–5 mm long, ca. 0.15 mm diam., glabrous or subglabrous. **Flowers** with calyx 2–4 mm long, sepals united only at the base, ca. 0.3 mm wide, glabrous; **corolla** 5–6.5 mm long, violet to purple or bluish purple, tube ca. 4 mm long, 1.5 mm diam.; ovary glabrous, style 2–3 mm long. **Fruits** 8–12 mm long, 0.9–1.2 mm wide, linear, smooth and bisulcate, drying blackish, apex acute, style deciduous or sometimes persisting; seeds 0.7–0.9 mm long, 0.3–0.4 mm diam., cylindrical with truncated ends, brown, the closely spaced ridges forming spirals around the surface.

Rarely collected plants of moist areas in open sunny sites, 0–1100 m elevation in Central Amer-

ica. Probably flowering primarily in the wet season, June–December. Only two Costa Rican collections have been seen: *A. Jimenez 984*, from near Playa Coco, Guanacaste, and *Tonduz 13790*, from Nicoya, Puntarenas. The species ranges from Mexico to northwestern Costa Rica and has been collected in Colombia.

Schistophragma mexicana is very distinctive because of its small stature, small opposite pinnatifid leaves with narrow lobes, small flowers with tubular purple or violet corollas, and dark linear fruits. This is the only Costa Rican species of Scrophulariaceae with linear fruits and one of the few with pinnatifid leaves (compare *Benjaminia* and *Castilleja*).

Scoparia Linnaeus

Herbs or subshrubs, annual or perennial, profusely branched, leafy stems slender, 4- to 6-angled. **Leaves** opposite or verticillate, 2–4/node, sometimes caducous or reduced to scales, petioles little differentiated from the blade, blades dentate to pinnatifid or entire, base cuneate, often glandular-punctate, venation pinnate. **Inflorescences** of 1 or 2 flowers in leaf axils (1–8/node), bracts and bracteoles absent, pedicels filiform. **Flowers** small, calyx 4- or 5-parted, sepals ovate to lanceolate, 1 often larger than the others; **corolla** subrotate with very short tube and 4 spreading or reflexed lobes (upper lip emarginate), white to blue, rose, or yellow, with a ring of hairs at the mouth of the tube; stamens 4, subequal or equal, inserted at the base of the tube, anthers sagittate with parallel or subequal thecae; ovary 2-locular, ovules many, style short, stigma subcapitate, exserted. **Fruits** thin-walled capsules, globose to ovoid, dehiscence septicial; seeds small, reticulate with pitted surface.

Scoparia is a Neotropical genus of ca. 17 species with centers of diversity in Mexico and southern South America. The plants are native to dry scrub and grasslands, and some species have become successful weeds. *Scoparia* is distinctive within the family because of its usually four-lobed corolla with very short tube and conspicuous hairs. Unfortunately, the corollas are fugaceous, and the characters of erect habit, solitary or paired flowers, four calyx lobes, and crenate or pinnatifid leaves must be used for identification. One species occurs in Costa Rica, and a second is likely to be found here.

Key to the Species of *Scoparia*

- 1a. Corolla white or pale lilac; sepals 4, obtuse or rounded at the apex; leaf blades to 35 mm long; plants usually becoming >40 cm tall; Mexico to Costa Rica *S. dulcis*
1b. Corolla yellow; sepals 4 or 5, acute at the apex; leaf blades to 20 mm long; plants <30 cm tall; Mexico to Nicaragua *S. annua*

Scoparia annua Schldl. & Cham., *Linnaea* 6: 375. 1831.

Small erect annual **herbs** 10–20(–30) cm tall, much-branched from the base or lower half, leafy stems 0.4–1.5 mm diam., glabrous, with 4 prominent longitudinal ridges. **Leaves** opposite, petioles not clearly differentiated from the blades, glabrous; **leaf blades** 5–20 mm long (including the narrowed base), lower blades ovate to rhombic and pinnatifid with rounded lobes to 4 mm long, distal blades linear-oblong and entire or with a few distal teeth, glandular punctate beneath. **Inflorescences** of solitary flowers in leaf axils (2/ node), pedicels 6–18 mm long, filiform, glabrous. **Flowers** with calyx 2 mm long, sepals 4- or 5-parted, lanceolate-oblong with acute apices, glabrous; **corolla** to 3 mm long, rotate, yellow, fugaceous, lobes 2 mm long, rounded; stamens equal, filaments glabrous; ovary ellipsoid, style shorter than the ovary, stigma minute. **Fruits** 2.5–3 mm long, 1.5–2 mm wide, ovoid, subtended by sepals ca. 3 mm long; seeds reticulate.

Scoparia annua ranges from Mexico to central Nicaragua in open sunny habitats from sea level to 1000 m elevation; it is also found in South America. These small weedy plants are likely to be overlooked, and it is possible that they will be found in northwestern Costa Rica.

Scoparia dulcis L., *Sp. Pl.* 116. 1753. Figure 4.

Herbs or subshrubs 0.3–1 m tall, woody at the base, often with many lateral branches, leafy stems 0.5–4 mm diam., 4- or 6-angled with 4 or 6 longitudinal ridges, glabrous or puberulent at the nodes, nodes with interpetiolar line. **Leaves** 2 or 3 (4) at each node, petioles 1–8 mm long (poorly differentiated), 0.3–0.9 mm wide; **leaf blades** 6–35 mm long, 2–15 mm wide, narrowly elliptic to oblanceolate (basal leaves ovate to ovate-rhombic), apex obtuse to acute, with 5–8 teeth/side distally, teeth 0.3–3 mm long, base obtuse to cuneate, drying grayish green, glabrous, glandular punctate on both surfaces, 2° veins 2 or 3/side.

Inflorescences of 1–3 flowers axillary to distal leaves (leaves often reduced to 6 mm long and bract-like), nodes with 2–6 flowers, pedicels 3–9 mm long, 0.1–0.2 mm diam., glabrous or minutely puberulent. **Flowers** with 4-parted calyx, 2 mm long (–3 mm in fruit), lobes ca. 1.3 mm long, elliptic to oblong, apex obtuse or rounded; **corolla** rotate and 3–4 mm wide distally, pale lilac or white, white-barbate within the throat; stamens ca. 1.5 mm long, anthers 0.7 mm long. **Fruits** 3 mm long, 2–3 mm diam., broadly ovoid, smooth, yellowish gray; seeds 0.3–0.4 mm long, 0.2–0.3 mm diam., oblong or irregularly angled, pale brown, pits in longitudinal rows.

Common plants of open sunny sites in deciduous, partly deciduous, and wet evergreen forest formations, 0–1300 m elevation. Flowering and fruiting throughout the year but collected most often in the wet season, June–December. The species ranges from the southeastern United States to southern South America and is a pantropical weed.

Scoparia dulcis is recognized by its short, much-branched herbaceous habit, nodes with usually two or three leaves, dentate leaf blades, small flower with white rotate corollas, and thin-walled fruits with pitted seeds. This species is a common weed in the lowlands of Central America. The bushy stems have been used to make small brooms and are believed to repel fleas (Standley & Williams, 1973). The plants have an aromatic odor and are called sweet broom; *culantrillo*, *escoba amarga*, *escobeta*, and *escobilla amarga* are Spanish names.

Sibthorpia Linnaeus

REFERENCE—O. Hedberg, A taxonomic revision of the genus *Sibthorpia*. *Bot. Not.* 108: 161–183. 1955.

Prostrate or creeping **herbs** rooting at many nodes, perennial, internodes often elongated, stems terete, with multicellular hairs, plants drying greenish or brown. **Leaves** alternate or crowd-

ed, petioles often long, slender, blades orbicular to reniform, margin crenate with broad rounded or truncated lobes, base cordate, villous to glabrous, venation palmate. **Inflorescences** of 1–3 flowers in axils of leaves, bracts and bracteoles absent, pedicels long and slender. **Flowers** very small, almost radially symmetric, calyx campanulate, united in the basal half with 5 (4–8) lobes, lobes subequal, acute, persisting in fruit; **corolla** subrotate with very short tube and 5 (4–8) spreading lobes, white, yellow, pink, or reddish purple, lobes rounded; stamens 2–8, as many as the corolla lobes or 1 or 2 fewer, borne near the apex of the tube, filaments slender, subequal, anthers slightly sagittate, thecae parallel or slightly divergent, confluent near the apex, staminodes absent; ovary pubescent, ovules few, style short, stigma simple or capitate. **Fruits** thin-walled capsules, dehiscence loculicidal; seeds few, oblong to ovate, convex on 1 surface, reticulate or smooth.

Sibthorpia is a genus of six species found in Europe, the high mountains of Africa, and higher elevations in the Neotropics. The creeping growth form, small alternate cordate reniform or orbicular leaves with crenate margins, very small axillary flowers, almost radially symmetric corolla, short corolla tube, and few-seeded capsules distinguish this genus. Seed morphology indicates that this genus is related to *Veronica*.

Sibthorpia repens (Mutis ex L.) Kuntze, Rev. Gen. Pl. 3: 239. 1898. *Willichia repens* Mutis ex L., Mant. Pl. 2: 558. 1771. *S. pichinchensis* Kunth in H.B.K., Nov. Gen. Sp. 2: 390, tab. 176. 1817. *S. triandra* Suesseng., Repert. Sp. Nov. Regni Veg. 39: 18. 1935.

Creeping **herbs**, usually with long internodes and few lateral branches, rooting at most nodes, leafy stems 0.5–1 mm diam., with slender translucent multicellular hairs 0.2–0.8 mm long, older stems usually glabrescent. **Leaves** alternate, petioles 2–22(–30) mm long, 0.3–0.8 mm diam., with translucent hairs to 0.8 mm long; **leaf blades** 6–22 mm long, 6.5–25 mm wide, ovate-suborbicular to rounded-reniform, apex a rounded lobe, margin crenate with 5–9 rounded or truncated lobes/side, lobes 0.5–4.5 mm wide, base cordate with sinus 1–7 mm deep, drying membranaceous, translucent hairs sparse to dense on both surfaces, major veins 3 or 5. **Inflorescences** of 1 (2) flowers in axils of leaves, pedicels 3–12 cm long (to 4 cm long in Mexico), filiform, puberulent. **Flowers** with calyx 1.7–2 mm long, united and campanu-

late, lobes 4 or 5, 0.5–1 mm long, acute; **corolla** 2–3 mm long, 3.5–5 mm wide, subrotate, pale lilac to dull purple to brown-purple or dark wine-red (white in Ecuador), tube very short, lobes 0.7–1.3 mm wide; stamens 2–4; style 2 mm long, stigma capitate. **Fruits** ca. 2 mm long, subglobose, lower part enclosed within the calyx cup, surface with straight ascending hairs 0.1–0.2 mm long, persisting style ca. 0.8 mm long; seeds ca. 0.7 mm long, oblong, dark with a whitish reticulum.

Rarely collected herbs of partly shaded to deeply shaded sites in evergreen montane forest formations, 1600–3100 m elevation. Collected with flowers in April–June (flowering primarily in December–March in northern Central America). These plants are locally common in open high-elevation forests of Guatemala, but we have seen only five collections from Costa Rica. This species ranges from central Mexico to Costa Rica and is found in the Andes.

Sibthorpia repens is recognized by the creeping habit, slender stems with many adventitious roots, small suborbicular leaves with lobed crenate margins, small axillary flowers, subrotate corollas with two epipetalous stamens, and few-seeded capsules enclosed at their base by the campanulate calyx. This species is quite variable in a number of significant taxonomic features. Despite this variability, it seems probable that, as Hedberg (1955, cited above) and Williams (1972) have suggested, the Neotropical material represents a single species. These plants are easily mistaken for species of *Hydrocotyle* (Apiaceae) or *Dichondra* (Convolvulaceae) with similar growth form.

Stemodia Linnaeus

Nomen conservandum

REFERENCES—B. Turner & C. Cowan, Taxonomic overview of *Stemodia* (Scrophulariaceae) for North America and the West Indies. *Phytologia* 74: 61–103. 1993. Taxonomic overview of *Stemodia* (Scrophulariaceae) for South America. *Phytologia* 75: 281–324. 1993.

Erect or procumbent **herbs** or shrubs to 3 m tall, annual or perennial, stems terete or angular, often much-branched, usually puberulent, often with gland-tipped hairs, drying greenish or brown. **Leaves** opposite, subopposite, or verticillate, simple, sessile or petiolate, blades serrulate to pinnately lobed (rarely subentire), pinnately veined or subpalmate, often glandular-punctate. **Inflorescences** of 1–3 flowers in axils of leaves or bracts (1–6/node), sometimes forming distal racemes, thyrses, or panicles, bracts absent when

flowers are subtended by leaves, pedicels slender, bracteoles present or absent at the base of the calyx. **Flowers** with deeply 5-parted calyx, sepals narrow and acute, equal or more often slightly unequal (adaxial sepal often larger), valvate in bud, persisting and enlarging slightly in fruit; **corolla** tubular to narrowly campanulate, 2-lipped, white to blue, lilac, or purple (yellowish when faded), 4- or 5-lobed, bilabiate, upper (adaxial) lip 2-lobed or entire, lower lip 3-lobed, often bearded at the base of the lobes; stamens 4, equal or of 2 unequal pairs, included, borne on the tube, filaments glabrous or puberulent, anthers glabrous, with an enlarged connective separating the 2 parallel or divergent thecae, a staminode sometimes present; ovary ovoid, style terete, stigma ligulate, often minutely 2-lobed or capitate and reflexed. **Fruits** dry capsules, often bisulcate, dehiscent loculicidally and partly septucidally from the apex (2- or 4-valved), placenta drying to form a peg that is free from the apex of the locule; seeds many, small, oblong to pyriform or irregular, often longitudinally sulcate or ridged, usually with a short stipe at one end.

According to Turner and Cowan (1993) *Stemodia* is a genus of 29 Neotropical and 20 Old World species, including several widespread weeds. They are placed in subfamily Antirrhinoideae, tribe Gratioleae, subtribe Stemodiinae. Because of the variability of important taxonomic characteristics within the genus, it is likely that *Stemodia* may be broken up into smaller genera (see *Darcya*). Minod (1918) split the genus into a number of genera that have generally not been accepted. His characters were often variable and his nomenclature was flawed, which, as much as his splitting, accounts for the lack of interest in his classification. We follow Turner and Cowan's treatment and their annotations. These generally short, weedy plants are recognized by their opposite or ternate leaves, one- to six-flowered nodes, calyx with narrow sepals united only near the base, tubular two-lipped bluish to purple or white corollas, and style often curved at the terminal stigma. Other important characters are the anthers with thecae slightly separated by an expanded connective, and the seeds often with longitudinal ridges or sulci.

Key to the Species of *Stemodia*

- 1a. Flowers and fruits borne on slender pedicels 6–19 mm long; corollas white to pink or yellowish (if flowers have a prominent calyx tube, see *Torenia*) 2
- 1b. Flowers and fruits subsessile or on pedicels < 4 mm long; corollas blue to purple 3
 - 2a. Flowers 7–9 mm long; fruits 4–5 mm long; plants to 20 cm tall *S. angulata*
 - 2b. Flowers 12–15 mm long; fruits 5–7 mm long; plants to 80 cm tall *S. peduncularis*
- 3a. Fruits at least 3 mm long; calyx 4–6 mm long; flowers on spike-like axes; leaves subsessile, larger leaves to 6 cm long and oblanceolate *S. durantifolia*
- 3b. Fruits 1.8–2.5 mm long; calyx 2–4 mm long; flowers in leaf axils; leaves petiolate, larger leaves to 2 cm long and ovate-triangular *S. verticillata*

Stemodia angulata Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1853: 22. 1854. *Stemodiaca angulata* (Oerst.) Kuntze, Rev. Gen. Pl. 2: 466. 1891. *Stemodia jorullensis* subsp. *reprians* Minod, Bull. Soc. Bot. Genève, ser 2, 10: 190. 1918. Figure 2.

Small **herbs** 5–20 cm tall, stems to 40 cm long, often much-branched, leafy stems 0.3–1.7 mm diam., pubescence of thin multicellular translucent hairs 0.2–1.2 mm long, slightly viscid. **Leaves** opposite, petioles 2–9 mm long, 0.2–0.5 mm wide, puberulent with thin whitish hairs; **leaf blades** 6–20 mm long, 3–18 mm wide, ovate to ovate-triangular or ovate-rhombic, apex obtuse or round-

ed, margin with 7–11 teeth/side, base broadly obtuse or truncate, glandular punctate and sparsely puberulent above and below, 2° veins 3–5/side, ascending. **Inflorescences** of 1 (2 or 3) flowers in leaf axils, pedicels 4–12 mm long (–19 mm in fruit), 0.1–0.2 mm diam., puberulent, bracteoles absent. **Flowers** with calyx 4–6 mm long, sepals 3–5 mm long, ca. 0.8 mm wide at the base, puberulent; **corolla** 7–9 mm long, white with purple lines within (yellowish in age), tube to 7 mm long, 1.4–2 mm diam., lobes to 2 mm long; stamen pairs very unequal, 2 borne at the base and 2 in the upper part of the tube. **Fruits** 4–5 mm long, ca. 2 mm diam., oblong, pale yellowish brown, glabrous; seeds 0.3–0.4 mm long, 0.2–0.3 mm

diam., variously shaped, brown to black, longitudinally sulcate with 6–8 ridges.

Plants of open sunny sites in both seasonally dry and wet evergreen forest areas, 10–1400 m elevation. Probably flowering and fruiting throughout the year, but collected most often in August–March. The species ranges from Mexico and the West Indies to northwestern South America.

Stemodia angulata is recognized by its short stature, opposite ovate-triangular leaves, solitary axillary flowers on slender pedicels, nearly separate sepals, and small white to rose corollas. Standley (1938) included this species under *S. peduncularis*, but that species, although similar, is larger in almost all its dimensions. In the *Flora of Panama*, specimens of this species were placed under *S. jorullensis* Kunth in H.B.K., a species of western Mexico.

Stemodia durantifolia (L.) Swartz, Obs. Bot. 240. 1791. *Capraria durantifolia* L., Syst. Nat. ed. 10: 1116. 1759. Figures 4 and 6.

Herbs 0.2–0.9(–1.5) m tall, annual or becoming woody at the base, usually with many branches, leafy stems 0.5–4.5 mm diam., pubescent with crooked translucent multicellular viscid glandular hairs 0.1–0.5 mm long, stems 4-angled with 4 longitudinal ridges. **Leaves** 2–3/node, diminishing in size distally and intergrading with the bracts, sessile and clasping the stem; **leaf blades** 1.4–7 cm long, 4–18 mm wide, smaller leaves narrowly elliptic-oblong to narrowly ovate, larger leaves oblanceolate, apex acute, margin with 3–12 teeth/side, base auriculate in larger leaves, both surfaces with minute (0.1 mm) glandular hairs and longer thin hairs, 2° veins 2–5/side. **Inflorescences** 4–17 cm long, spicate or paniculate to 50 cm long with opposite spicate branches and internodes 5–15 mm long, puberulent like the stems, bracts (reduced leaves) 5–16 mm long, 2–5 mm wide, pedicels 0–3 mm long, bracteoles 1 or 2, subtending the calyx, linear, 2–5 mm long. **Flowers** with calyx 4–6 mm long, ca. 1 mm diam., lobes 2–4 mm long, linear-lanceolate, densely glandular-puberulent; **corolla** 5–7 mm long, blue to purple, glandular-puberulent, tube ca. 1 mm diam., yellow within the throat, lower lobes ca. 1.5 mm long; stamens inserted at the same level near the mouth of the tube, connective globose; style 3–4 mm long. **Fruits** 3–4 mm long, 2 mm diam., narrowly ovoid, smooth, yellowish brown; seeds 0.2–0.3 mm long, 0.15 mm diam., narrowly oblong or nar-

rowed at one end, dark brown, with longitudinal rows of rounded tubercles (50×).

Weedy plants of open sunny moist sites or partly shaded woodland in seasonally dry vegetation of the Pacific slope (rarely collected on the Caribbean slope), 0–900 m elevation. Flowering and fruiting throughout the year, but collected most often in November–March. The species ranges from the southwestern United States, Mexico, and the West Indies to Chile and Brazil.

Stemodia durantifolia is recognized by the erect, much-branched, weedy habit, viscid pubescence, sessile leaves with basal blades oblanceolate, long distal spikes with short internodes, small flowers, and blue or purple corollas. The flowers are usually two per node but may be as many as six per node. Distal bracts may be alternate or tightly congested on flowering stems. The bracteoles are difficult to distinguish from the sepals but are an unusual character. These plants resemble species of *Hyptis* (Lamiaceae).

Stemodia peduncularis Benth. in DC., Prodr. 10: 382. 1846. *Stemodiocris peduncularis* (Benth.) Kuntze, Rev. Gen. Pl. 2: 466. 1891. Figure 3.

Erect or decumbent **herbs** 10–80 cm tall, usually with few or no lateral branches on distal stems, leafy stems 0.5–2 mm diam., pubescence of thin white or viscid hairs 0.2–0.5 mm long, glabrescent. **Leaves** opposite, petioles 4–14 mm long, 0.3–0.9 mm wide, puberulent with thin whitish hairs, leaf base decurrent on the petiole; **leaf blades** 8–40(–50) mm long, 6–25(–35) mm wide, ovate to ovate-triangular or ovate-oblong, apex acute, margin with 8–12 teeth/side, base obtuse to truncate, punctate and minutely (0.1–0.2 mm) puberulent on both sides, 2° veins 3 or 4/side, strongly ascending. **Inflorescences** of 1 or 2 flowers in leaf axils (1–4/node), pedicels 6–18 mm long (–50 mm in fruit), 0.1–0.2 mm diam., with thin whitish hairs 0.1–0.2 mm long. **Flowers** with sepals 4–7 mm long, 0.7–1 mm wide at the base, linear to linear-triangular, minutely puberulent (sometimes glandular punctate); **corolla** 11–15 mm long, white or red-veined (yellowish), tube 8–10 mm long, 2–3 mm diam., externally glabrous, lobes 2–3 mm long; stamens borne near the base of the tube; style 4–7 mm long. **Fruits** 5–7 mm long, narrowly ovoid; seeds 0.5–1 mm long, irregular in shape, black.

Inrequently encountered plants of shaded sites in moist evergreen montane forest formations along the Continental Divide and Pacific slope in

the central volcanic highlands and Cordillera de Talamanca, 1300–2400 m elevation. Flowering and fruiting throughout the year, but collected mostly in December–March. The species ranges from western Mexico to western Panama.

Stemodia peduncularis is recognized by its short, erect, few-branched habit, opposite serrate leaves, mostly solitary flowers on long slender pedicels, separate linear sepals, and white tubular corollas. Standley (1938) incorrectly included *S. angulata* under this species. This species resembles our species of *Darcya* in general appearance.

Stemodia verticillata (Miller) Hassler, Trab. Mus. Farmacol. 21: 110. 1909. *Erinus verticillatus* Miller, Gard. Dict. ed. 8. 1768. *S. parviflora* W. T. Aiton, Hortus Kew., ed. 2, 4: 52. 1812. *S. arenaria* Kunth in H.B.K., Nov. Gen. Sp. 2: 357. 1817. *Lindernia verticillata* (Miller) Britton in Britton & Wilson, Bot. Porto Rico 6: 184. 1925. Figure 2.

Small **herbs** 5–15(–25) cm tall, prostrate to ascending, rooting only near the base, internodes mostly 4–14 mm long, leafy stems 0.5–1 mm diam., densely puberulent with straight or curved (often glandular) hairs 0.2–0.8 mm long. **Leaves** usually 2 or 3 (4) per node, petioles 2–11 mm long, 0.2–0.5 mm wide, puberulent, leaf base decurrent on the petiole; **leaf blades** 5–12(–18) mm long, 3–10(–14) mm wide, ovate to ovate-triangular or ovate-oblong, apex obtuse, margin with 5–9 teeth/side, teeth ca. 0.5 mm long, base obtuse or truncated, both surfaces with hairs 0.1–0.5 mm long, 2° veins 3–5/side. **Inflorescences** of usually 2 subsessile axillary flowers (2–6/node), pedicels 0.5–2 mm long, minutely puberulent, bracteoles absent. **Flowers** with calyx 2–4 mm long, sepals equal or subequal, 0.5 mm wide near the base, with thin whitish and glandular hairs; **corolla** 3–5 mm long, blue-violet or purple with white throat, tube 1 mm diam., lobes 1–2 mm long; stamens borne in the lower half of the tube, anther thecae 0.3 mm long; style 1–1.5 mm long with recurved stigma. **Fruits** 1.8–2.5 mm long, 1.4–2 mm wide, ovoid-subglobose, glabrous, pale yellow-brown; seeds ca. 0.5 mm long, 0.2–0.3 mm diam., narrowly ovoid, yellowish, with dark tip 0.05 mm long, surface with longitudinal ridges and sulci.

Uncommon weeds of open sunny or shaded sites (often on sand or wet gravel) in evergreen or deciduous vegetation, 0–1600 m elevation. Probably flowering and fruiting throughout the

year, but collected in Costa Rica primarily in July–August. The species ranges from Mexico and the West Indies to Argentina.

Stemodia verticillata is recognized by its small, often prostrate habit, mixture of both glandular and eglandular hairs, small petiolate leaves subtending solitary subsessile flowers, narrow sepals, and bluish or purple corollas. Plants with three or four leaves per node are distinctive. The glandular punctations of the leaf surfaces are often obscure. These plants have been called *hierba santa* (Costa Rica) and *corrimiento* (El Salvador).

Tetranema Benthham ex Lindley

REFERENCES—M. Grayum & B. Hammel, The genus *Tetranema* (Scrophulariaceae) in Costa Rica, with two new species. *Phytologia* 79: 269–280. 1995 (1996). T. Méndez-Larios & J. Villaseñor. Revisión taxonómica del genero *Tetranema* (Scrophulariaceae). *Acta Bot. Mexico* 32: 53–68. 1995.

Herbs, erect or decumbent, perennial, sometimes woody at the base but the stems usually short, glabrous or pubescent. **Leaves** opposite and often crowded near the base, equal or unequal at a node, subsessile and clasping the stem or petiolate, blades dentate to subentire, venation pinnate. **Inflorescences** axillary, cymose to subumbellate or congested, long-pedunculate, bracteate, pedicels short but often elongating in fruit. **Flowers** with the calyx deeply 5-parted, campanulate, lobes narrow and attenuate-acuminate, with prominent longitudinal ribs; **corolla** tubular to campanulate, 2-lipped, glabrous, white to rose, purple or less often red, tube longer than the lobes, upper lip emarginate (1-lobed), lower lip with 3 spreading lobes, imbricate in bud; stamens 4 (rarely 3), filaments of 2 longer and 2 shorter pairs, anthers 2-theous, a staminode very small (in ours) or absent; ovary 2-locular, style slender or thick, stigma capitate or bilobed. **Fruits** capsules, ovoid to globose, glabrous, dehiscence loculicidal; seeds many, angled or tetrahedral, surface reticulate or foveolate.

Tetranema is a genus of six species from Mexico and Central America. It is distinguished by its opposite leaves, axillary and cymose inflorescences, separate sepals, four-lobed and two-lipped corolla, and loculicidal capsules. Our recently discovered species are unusual in having red (probably hummingbird-pollinated) flowers. These distinctive plants (Fig. 27) may resemble *Razisea*

spicata Oerst. and *Odontonema tubaeforme* (Ber-
tol.) Kuntze of the Acanthaceae. The Costa Rican
species are similar to *T. megaphyllum* (Brandee-
ge) L. O. Williams, but that species has smaller
(2–4 mm) corolla lobes and larger (6–10 mm) floral
bracts and is endemic to Mexico. Species of
Tetranema are sometimes cultivated as ornamen-

tals, especially *T. roseum* (M. Martens & Galeoti)
Standl. & Steyerem. The new species come from
the Pacific slope of central Costa Rica and both
slopes of southern Costa Rica. The dichotomy in
Flora of Guatemala separating *Tetranema* from
Penstemon and *Uroskinnera* is inverted (Standley
& Williams, 1973, p. 321).

Key to the Species of *Tetranema*

- 1a. Inflorescences with 14–30 flowers, peduncle purple; corollas 26–35 mm long, pubescent internally with a band of flat yellow hairs along the entire ventral (abaxial) surface and onto the lower lobe; leaf apex rounded to short-acuminate; 1200–1600 m on Cerro Turrubares *T. floribundum*
1b. Inflorescences with 2–12 flowers, peduncle green; corollas 44–55 mm long, glabrous throughout or rarely pubescent on the lower lobe and mouth; leaf apex long-acuminate; 500–1200 m elevation on both Caribbean and Pacific slopes *T. gamboanum*

Tetranema floribundum B. Hammel & M. Grayum, *Phytologia* 79: 269–280. 1995 (1996). Figure 27.

Erect herbs (0.3–)0.8–2 m tall, decumbent near the base and often rooting at the lower nodes, internodes to 5 cm long, arachnoid or wooly-pubescent when young, leafy stems 1.5–5 mm thick, glabrescent. **Leaves** opposite, sessile with petioles 0–6 mm long, ca. 2 mm thick; **leaf blades** 14–24 cm long, 7–13 cm wide, broadly elliptic to oblanceolate or spatulate, apex abruptly acute or short-acuminate, margins coarsely serrate or undulate-toothed with teeth ca. 1 mm high, base gradually cuneate, mostly glabrous above, minutely puberulent on the major veins beneath, lustrous beneath when dry, 2° veins 8–11/side, ascending. **Inflorescences** 15–30 cm long, 14–30-flowered, peduncles 13–23 cm long, purple, with 4 longitudinal ridges, bracts 1–5 mm long, narrowly triangular, margins ciliate (often only at the base), pedicels 10–20 mm long, glabrous. **Flowers** with calyx ca. 3 mm long (–5 mm in fruit), divided nearly to base, striate and glabrous (except along margins), with a short apical projection; **corolla** 26–35 mm long, 5–6 mm diam., tubular and slightly expanded distally and curved upward, red-orange, lobes 4, ca. 13 mm long, 2.5–5.5 mm wide, the 3 lower rounded apically and reflexed-spreading, puberulent internally abaxially; stamens slightly exerted, anthers 0.8–0.9 mm long, staminode ca. 0.5 mm long; ovary ca. 3.5 mm long. **Fruits** not seen at maturity, ca. 8 mm long, ovoid, borne on pedicels ca. 20 mm long.

Plants of evergreen lower montane forest for-

mations at 1200–1600 m elevation on Cerro Turrubares. Flowering in December–January and March. This species is known only from an isolated peak on the Pacific slope of the southeastern part of the central plateau in the province of San José.

Tetranema floribundum is recognized by its larger subsessile elliptic to obovate leaves with many ascending secondary veins, inflorescences with long purple peduncles, five separate acute sepals, curved-tubular red corollas, and isolated habitat. Cerro Turrubares is also the location of a recently discovered and unusual species of *Psychotria* (Burger & Jiménez, 1994).

Tetranema gamboanum M. Grayum & B. Hammel, *Phytologia* 79: 269–280. 1995 (1996). Figure 27.

Erect herbs 1–2 m tall, internodes to 11 cm (or more) long, at first minutely strigulose, 1.7–5 mm thick, glabrous but with a puberulent interpetiolar line. **Leaves** opposite, sessile to subsessile or with petioles to 1 cm long, canaliculate above, margins ciliate at the base; **leaf blades** 14–31 cm long, 5–11 cm wide, elliptic to elliptic-obovate, apex long-acuminate, margin coarsely serrate with teeth 1–2 mm high, base cuneate and abruptly narrowed at the base, glabrous above or with few hairs along midvein and major veins, minutely puberulent along the veins beneath, 2° veins 9–13/side. **Inflorescences** axillary cymes with 2–13 flowers, peduncles 9–24 cm long, green, quadrangular with 4-winged ribs, bracts 0.5–2 mm long, subulate to narrowly triangular, ciliate along the margins, pedicels 9–12 mm long (–20 mm in fruit),

glabrous. **Flowers** with 5-parted calyx, sepals 3–5 mm long (–6 mm in fruit), inner 2 sepals slightly smaller than the outer, narrowly to broadly ovate, imbricate in bud, minutely ciliolate along the margin, apex acute, venation parallel; **corolla** 44–55 mm long, ca. 5 mm diam., narrowly tubular, gradually expanded distally and slightly curved, bright red, glabrous throughout or with hairs at throat and lower lobes, lobes 8–14 mm long, 3–4 mm wide, lanceolate or oblong, the 3 lower lobes obtuse to rounded at the apex and spreading-reflexed; stamens slightly exerted, filaments dilated near base, glabrous, anthers 0.8–1 mm long, with divergent thecae confluent at the base, staminode 1.5–2 mm long; ovary 3–4 mm long, narrowly ovoid, style exerted, stigma capitate. **Fruits** capsules, 6–9 mm long (not including the 1–2 mm style base), subglobose-apiculate, glabrous; seeds 0.5–0.7 mm long, 0.4–0.5 mm diam., rectangular or oblong-rounded, surface with prominent pits (foveolate), dark yellow to brown or blackish.

Newly discovered plants of evergreen rain forest formations on the Caribbean slope of the Cordillera de Talamanca and on the southern Pacific slope, 500–1200 m elevation. Flowering and fruiting in December–May. This species has been collected only from between 83°W and 84°W in the southern half of Costa Rica.

Tetranema gamboanum is distinguished by its erect stems with larger ellipsoid leaves with many lateral veins, axillary cymes on long peduncles, five-parted calyx, and bright red, slightly curved corolla tubes.

Torenia Linnaeus

Annual or perennial **herbs**, erect or procumbent, branching from both basal and distal nodes,

Key to the Species of *Torenia*

- 1a. Corolla 30–40 mm long, lower lobes dark purple or blue-violet; calyx broadly winged and 5–10 mm wide; leaves 16–50 mm long, often truncate at the base *T. fournieri*
- 1b. Corolla 7–12 mm long, lower lobes pale purple or pale blue-violet; calyx not winged, 2–3 mm diam.; leaf blades 8–22 mm long, obtuse to rounded at the base *T. thouarsii*

Torenia fournieri Linden in Fourn., *Illustr. Hortic.* 23: 129, tab. 249. 1876. Figure 8.

Weak-stemmed erect **herbs** 15–50 cm tall, often reddish near the base, main stems with 2–5 branching nodes, leafy stems 1–3 mm diam., 4-

stems 4-angled with longitudinal ridges, puberulent to hirsute or glabrous. **Leaves** opposite, petiolate, blade margins entire to serrate or crenulate, venation pinnate. **Inflorescences** of 1–3 flowers in axils of distal leaves or in short terminal or axillary few-flowered racemes, linear bracts sometimes present, pedicels usually held at a 45° angle to the stem. **Flowers** showy or small, calyx usually somewhat shorter than the corolla tube, united to form a long tube with 3–5 short lobes (or 2-lipped), with 3–5 longitudinal ribs or broad wings, persisting and enlarging in fruit; **corolla** campanulate to tubular or salverform, bilabiate with the upper lip erect and 2-lobed, lower lip with 3 lobes, tube usually widened distally, bearded in the throat; stamens 4, in 2 unequal pairs, filaments inserted near the top of the tube and usually with a tooth-like appendage at the base, anterior 2 arching upward over the stigma (with anthers connivent or reduced), thecae oblong to linear, divaricate by the enlarged connective; disc prominent and saucer-shaped or cupulate; ovary oblong, style straight, stigma slightly 2-lobed. **Fruits** capsules, usually enclosed within the persisting perianth tube, oblong-ellipsoid, dehiscent septically to the base, placenta linear with septum forming wings; seeds globose to variously angled, tuberculate or reticulate.

Torenia is a genus of 40 to 80 species of tropical Africa and Asia. A few species are cultivated ornamentals that have become naturalized in the Americas. *Torenia* is closely related to *Lindernia*, sharing the curved appendaged filaments often found in that genus. Species of *Torenia* in the New World can be distinguished from *Lindernia* by their larger flowers, tubular calyx, elongate fruits, and globose pitted seeds.

angled with prominent longitudinal ridges, nodes with thin whitish hairs 0.2–0.5 mm long (internodes often glabrous). **Leaves** opposite throughout, petioles 3–17 mm long, 0.7–1.4 mm wide, with thin whitish hairs along the adaxial margins; **leaf blades** 16–50 mm long, 6–25 mm wide, tri-

angular to ovate-triangular or ovate-elliptic, apex acute, margin with prominent teeth, base truncate to obtuse, upper surface with few thin straight hairs 0.2–0.5 mm long, 2° veins 3–6/side, strongly ascending. **Inflorescences** of solitary flowers in distal leaf axils (2/node) or more often in short terminal racemes with 4–8 flowers, bracts 2–5(–12) mm long, linear, pedicels 4–18 mm long, 0.6–1 mm wide, glabrous or very sparsely puberulent. **Flowers** with calyx 13–22 mm long, 5–10 mm wide, tube more than half the calyx length, broadly winged to produce an ovate form with acute or acuminate apices, ciliolate; **corolla** 3–4 cm long, 2–3 cm wide distally, tube 7–9 mm diam. in the center, whitish near the base, upper lip often pale blue with the lower lobes very dark blue-violet, a yellow patch present within at the base of the central lobe. **Fruits** 1–2 cm long, included within the slightly enlarged calyx.

Torenia fournieri, a native of southeastern Asia, is widely planted as an ornamental. This species may become naturalized in lowland and mid-elevation areas of Central America, but it seems doubtful that the populations persist for long. These plants are easily distinguished by their small size, opposite (often triangular) leaves, few-flowered racemes, broadly winged calyx, and relatively large corollas with dramatic dark purple-violet coloring. This species is unusual within the genus in having broadly winged sepals and in lacking basal appendages on the lower filaments. *Torenia asiatica* L. is similar but has prostrate stems. The large colorful corollas make these plants especially attractive. They can be mistaken for members of the Gesneriaceae.

Torenia thouarsii (Cham. & Schldl.) Kuntze, Rev. Gen. Pl. 2: 468. 1891. *Nortenia thouarsii* Cham. & Schldl., Linnaea 3: 18. 1828. *Lindernia thouarsii* (Cham. & Schldl.) Edwin, Phytologia 19: 361. 1970. Figure 3.

Procumbent or erect **herbs** 10–30 cm tall, leafy stems 0.6–1.3 mm diam., quadrangular, internodes glabrous or with thin whitish hairs 0.2–0.5 mm long, nodes usually with thin hairs. **Leaves** opposite throughout, petioles 1–7 mm long, ca. 1 mm wide with thin lateral margins, sparsely puberulent; **leaf blades** 8–22 mm long, 5–12 mm wide, ovate-elliptic to ovate-triangular, apex acute, margins with 4 or 5 prominent teeth/cm, base obtuse to rounded, surfaces glabrous or sparsely puberulent, 2° veins 3–5/side, arcuate ascending. **Inflorescences** of 1 or 2 flowers axillary

to foliage leaves (1–4/node), bracts ca. 2 mm long, linear, pedicels 2–15 mm long, ca. 0.5 mm diam., glabrous or sparsely puberulent. **Flowers** with calyx 4–12 mm long, 1.3–2 mm diam. (to 18 × 3 mm in fruit), narrowly tubular to tubular-ellipsoid, glabrous, lobes 2–3 mm long, acute; **corolla** 7–12 mm long, bluish, purple, or white, lobes crenate; filaments with a linear appendage at base, staminode with a rounded tip. **Fruits** 8–10 mm long, 2–3 mm wide, narrowly oblong-ellipsoid, included within the enlarged calyx tube or the tube splitting.

Torenia thouarsii, a native of India, is naturalized in parts of Central and South America. In Costa Rica it is occasionally found in wet sites at 10–2000 m elevation, from the Caribbean lowlands to the central highlands. These plants resemble species of *Lindernia* and *Stemodia* but differ in the tubular calyx and narrowly oblong fruits.

Veronica Linnaeus

Annual or perennial **herbs** (rarely shrubs), prostrate or ascending to erect, often branching from the base, stems terete or with longitudinal ridges, glabrous or puberulent. **Leaves** opposite near the base and usually alternate distally, sometimes intergrading with smaller floral bracts, sessile or petiolate, blades subentire to dentate, crenate or divided, pubescence of simple multicellular or glandular hairs, venation usually palmate or subpalmate. **Inflorescences** of solitary flowers in leaf axils or of elongate racemes (or spike-like) with flowers solitary in the axils of bracts, usually terminal, pedicels very short to long and slender. **Flowers** mostly small, calyx deeply 4-lobed (rarely 5-lobed), the lobes (sepals) subequal to unequal, slightly overlapping in bud, usually persisting and slightly enlarged in fruit, glabrous or puberulent; **corolla** rotate (rarely campanulate), tube very short, corolla lobes 4 (5), unequal, with the lower lobe the smallest, lateral lobes exterior in bud, blue to purple or white (rarely reddish); stamens 2, borne at either side of the upper lobe, exerted, filaments attached at the base of the tube and free, anthers 2-thecous, thecae confluent at the apex; ovary rounded, 2-locular, ovules few to many, style simple, persisting in fruit but not enlarging, stigma capitate. **Fruits** capsules, flattened at right angles to the plane of the septum, obovoid or 2-lobed (obcordate) with a depressed or emarginate apex, dehiscence loculicidal (also sometimes septicidal); seeds few to many, ovate to or-

bicular, surfaces smooth to rugulose, often with the inner face concave, embryo often U-shaped.

Veronica is a genus of 150 to 250 species confined to cool climates. The great majority of species are found in Europe and Asia, but a number have become widespread weeds; it seems likely that none are native to Central America. The genus is distinguished (in our area) by its small herbaceous growth form, small leaves becoming alternate distally, small flowers with prominent calyx lobes (sepals), bluish to lilac or white corollas with the four lobes usually held in a single plane (rotate), two stamens, and unusual fruits. The cap-

sules are flattened perpendicular to the plane of the septum and often have an emarginate or deeply notched apex. The rounded lateral lobes of the fruits (carpels) can be lenticular or rounded. The genus is placed in the tribe Veroniceae and is closely related to *Sibthorpia* and the Australasian *Hebe*. Unfortunately, some species of *Veronica* are very similar, and a number of Central American collections have been misidentified in the past. In Costa Rica the genus has not been found below 1200 m elevation, and only two species (*V. polita* and *V. serpyllifolia*) are commonly collected.

Key to the Species of *Veronica*

- 1a. Flowers borne on conspicuous pedicels, the pedicels much longer than the calyx lobes, flowers arising from the axils of leaves or from short axillary racemes; leaves with prominent teeth along the margins; styles 1.3–3 mm long 2
- 1b. Flowers borne on short pedicels, the pedicels much shorter to slightly longer than the calyx lobes, flowers arising from the axils of leaves or from the axils of floral bracts differing greatly in size and form from the basal leaves; leaves with small or inconspicuous teeth along the margin (except in *V. arvensis*); styles 0.5–2.5 mm long 3
 - 2a. Corolla < 8 mm wide; fruits about as broad as long, ca. 4 mm wide, venation obscure; fruiting sepals ca. 5 mm long; leaf blades often triangular-ovate; styles 1.3–1.6 mm long; occasional at 1400–3300 m elevation *V. polita*
 - 2b. Corolla 8–13 mm wide; fruits distinctly broader than long, 5–9 mm wide, venation prominent; fruiting sepals ca. 6 mm long; leaf blades usually ovate-oblong; styles 1.8–3 mm long; rarely collected in Costa Rica *V. persica*
- 3a. Lower leaf blades 8–28 mm long, narrowly oblanceolate, leaves gradually intergrading into the smaller distal floral bracts; erect stems to 45 cm tall; corolla white with purple lines [pedicels ca. 1 mm long; styles ca. 0.5 mm long; rarely collected in southern Central America] .. *V. peregrina*
- 3b. Lower leaf blades up to 12 mm long, usually broadly ovate; leaves usually clearly differentiated from the smaller floral bracts; erect stems rarely exceeding 20 cm in height; corolla usually bluish 4
- 4a. Pedicels becoming 6 mm long; styles 1.8–2.5 mm long; margins of leaf blades subentire to slightly crenate; frequent in Costa Rica *V. serpyllifolia*
- 4b. Pedicels 0.5–1.2 mm long; styles ca. 0.6 mm long; margins of leaf blades minutely to conspicuously dentate-crenate; rarely collected in Costa Rica *V. arvensis*

***Veronica arvensis* L., Sp. Pl. 13. 1753.**

Annual **herbs**, 5–20(–40) cm tall, stems usually branching only near the base, leafy stems 0.4–1.3 mm diam., puberulent with thin curved whitish hairs 0.2–0.7 mm long. **Leaves** opposite (but bracts of the inflorescences alternate), sessile or the basal leaves with petioles 1–4 mm long; **leaf blades** 4–12 mm long, 3–10 mm wide, broadly ovate to ovate-oblong, apex obtuse or rounded, margin crenate-dentate with 2–6 teeth 0.3–0.8 mm high, base obtuse or truncate, with thin hairs

ca. 0.5 mm long on both surfaces, venation palmate with 3 or 5 major veins. **Inflorescences** erect spike-like racemes, 2–15 cm long, bracts 4–7 mm long, 1–2 mm wide, narrowly oblong to narrowly ovate, narrowed at the base, rachis 0.5–1.2 mm diam., puberulent, pedicels 0.5–1.2 mm long. **Flowers** with unequal calyx lobes 2.5–4 mm long (becoming 5 mm long in fruit), ca. 1 mm wide, narrowly oblong to narrowly elliptic-oblong, puberulent with short thin hairs; **corolla** blue, upper lobe ca. 2 mm long; anthers ca. 0.4 mm long; styles ca. 0.6 mm long. **Fruits** 3.5–4 mm long,

ca. 3.5 mm wide, lenticular-obovoid, distally bilobed with an apical notch 0.5–1 mm deep, puberulent along the margin.

Veronica arvensis is found on the slopes of Volcán Turrialba (Khan *et al.* 1977), but it is rarely collected in Central America. This species is recognized by its short stature, leaves with subentire margins, very short pedicels, and blue corollas. The closely clustered bracts and calyx lobes give the inflorescences of this species a spike-like appearance. Also, there are few intermediate leaves along the stem between the lower foliage leaves and the much narrower floral bracts in this species.

Veronica peregrina L., Sp. Pl. 14: 1753. *V. xalapensis* Kunth in H.B.K., Nov. Gen. Sp. 2: 389. 1817. *V. peregrina* var. *xalapensis* (Kunth in H.B.K.) Pennell, Torreya 19: 167. 1919.

Erect or spreading **herbs** 5–45 cm tall, branching mostly near the base, leafy stems 0.3–3 mm diam., glabrous (in var. *peregrina*) or with minute (0.2 mm) gland-tipped hairs (in var. *xalapensis*). **Leaves** opposite near the base and alternate distally, gradually becoming smaller and bract-like distally, narrowed at the base but a petiole not clearly differentiated; **leaf blades** 8–28 mm long, 1–8 mm wide, narrowly oblong to narrowly elliptic-oblong or oblanceolate (spatulate), apex bluntly acute or rounded, margin entire or with few small teeth, base gradually narrowed and cuneate, surfaces glabrous, venation subpalmate with a prominent midvein. **Inflorescences** of solitary flowers in leaf axils or flowers in the axils of reduced bract-like distal leaves, spike-like with pedicels ca. 1 mm long, rachis sparsely puberulent. **Flowers** with subequal or strongly unequal calyx lobes ca. 4 × 1 mm (–6 mm long in fruit), narrowly oblong, sparsely puberulent; **corolla** 2–3 mm wide, white marked with purple lines; stamens 2–3 mm long; style ca. 0.5 mm long. **Fruits** 2.8–4 mm long, 4–5 mm wide, obovoid-triangular with a slight indentation at the apex, compressed-lenticular, glabrous or puberulent.

Plants of open moist sites, often along riverbeds, 1000–3000 m elevation. Probably flowering throughout the year in northern Central America, but rarely collected in southern Central America. This species is native to southern Europe and is now widely naturalized in temperate climates.

Veronica peregrina is recognized by its white flowers, longer erect spicate stems, and narrowly oblong subentire leaves. Although glabrous in Eu-

rope, plants in the Americas range from glabrous to glandular puberulent (var. *xalapensis*). The typical glabrous variety is more common in the eastern United States, whereas var. *xalapensis* is most common in the western United States, Mexico, and Central America, but they intergrade, and both varieties can be found in a broad band across the central United States. The longer distal stems are unusual in that there is a gradual change from flowers subtended by narrow leaves (to 3 cm long) to flowers subtended by linear bracts only 6 mm long.

Veronica persica Poirlet in Lam., Encycl. 8: 542. 1808. *V. rotundifolia* Sesse & Mociño, Fl. Mex. 5: 1892.

Creeping **herbs**, stems 5–30(–50) cm long (–15 cm tall), leafy stems 0.5–2 mm diam., puberulent with thin whitish hairs 0.1–0.5 mm long, often in longitudinal rows. **Leaves** opposite near the base and alternate throughout the distal stems, petioles 1–7 mm long, puberulent; **leaf blades** ovate to ovate-orbicular, 6–24 mm long, 4–16 mm wide, apex obtuse to rounded, margin with 3–6 prominent (0.5–2 mm) serrate lobes/side, base obtuse or truncate, surfaces with whitish hairs to 0.7 mm long, venation palmate with 3 or 5 major veins. **Inflorescences** of solitary flowers in leaf axils (bracts absent), pedicels 10–35 mm long, 0.2–0.3 mm diam., puberulent. **Flowers** with 4-parted calyx, sepals 4–5 mm long, subequal, to 6 mm long in fruit, 1–1.5 mm wide at the base, lanceolate, surfaces glabrous but the margin ciliolate; **corolla** 8–13 mm wide, upper lobe ca. 4 mm wide, pale blue or lilac with darker blue lines; filaments 2–3 mm long, anthers 0.9 mm long; style 1.8–3 mm long. **Fruits** 3.5–5 mm long, 5–9 mm wide, broadly obovate with apical notch and divergent lateral sides, surface glabrous or with thin hairs, the veins becoming prominent; seeds ovoid, flattened, rugulose.

Veronica persica, probably a native of the Caucasus and southwestern Asia, is now naturalized over much of northern North America and is rarely found at higher elevations in Mexico and Central America. Standley reported this species as growing on the slopes of Volcán Irazú in Costa Rica. This species is recognized by its creeping habit, solitary flowers in leaf axils, and larger obovate capsules that are distinctly broader than long. The broad fruit causes the persisting sepals to spread wide as the fruit matures. This species has often been confused with *V. polita*, but that

species has smaller flowers and different fruits. Material cited as *V. polita* in *Flora of Guatemala* and *Flora of Panama* is actually *V. persica*.

Veronica polita Fries, Novit. Fl. Succ. 63. 1819. Figure 2.

Creeping or vining **herbs**, stems 5–70(–120) cm long, branching at both distal and basal nodes, leafy stems 0.4–1.5 mm diam., appressed puberulent with thin whitish hairs 0.1–0.2 mm long. **Leaves** opposite, petioles 4–18 mm long, 0.3–0.6 mm wide and expanding at the blade, appressed puberulent; **leaf blades** 6–22 mm long, 6–22 mm wide, triangular to ovate-triangular, apex acute to obtuse, margins with 4–8 prominent teeth 0.3–3 mm high, base truncate to subcordate, surfaces with scattered stiff sharp hairs 0.1–0.7 mm long, venation palmate with 3 major veins. **Inflorescences** of solitary flowers in axils of leaves or of short (2–4 cm) axillary racemes with narrowly elliptic bracts 2–4 mm long, pedicels 3–15 mm long, 0.2–0.3 mm diam., puberulent. **Flowers** with calyx lobes (sepals) 4, subequal or with 1 distinctly smaller, lobes 3–4 mm long (–5 mm in fruit), 1.5–2 mm wide, narrowly obovate or obovate, surfaces subglabrous but margins with stiff curved hairs; **corolla** 4–5 mm long, less than 8 mm wide at anthesis, blue with linear darker markings, filaments ca. 1.3 mm long, anthers 0.4 mm long; styles 1.3–1.6 mm long. **Fruits** ca. 3 mm long, 3–4 mm wide, obovate-triangular or slightly obcordate, veins usually indistinct; seeds obovoid, with one flattened face, rugulose to ridged.

Plants of open moist slopes, damp disturbed sites, and partly shaded forest floor, 1400–3000 m elevation. Flowering and fruiting throughout the year. This species is a native of Europe that is now widely naturalized in North America and montane areas in Central America.

Veronica polita is distinguished by its often triangular leaves with prominent teeth, flowers in axils of leaves or on short axillary racemes, well-developed pedicels, and blue corollas not extending much beyond the obovate sepals. In addition, the stems are often long and much-branched, and many parts have short sharp hairs. There has been a controversy over the correct name for this species. An earlier name, *V. didyma* Tenore, has been used for this species, but many European authors consider that name a nomen ambiguum and reject it in favor of *V. polita*. This species is closely related to *V. persica*.

Veronica serpyllifolia L., Sp. Pl. 12. 1753. *V. tenella* All., Fl. Pedemont. 1: 75. 1785. *V. humifusa* Dickson, Trans. Linn. Soc. 2: 228. 1794. *V. serpyllifolia* var. *humifusa* (Dickson) Vahl, Enum. Pl. 1: 65. 1805. *V. crenulata* Sesse & Mociño, Fl. Mex. 5. 1892, non Ruiz & Pavón 1798. Figure 2.

Small **herbs** 5–20 cm tall, erect stems unbranched, sometimes with repent sterile leafy branches forming small mats, leafy stems 0.5–0.9 mm diam., puberulent with thin ascending whitish hairs 0.1–0.2 mm long. **Leaves** opposite in the lower half of the stem, alternate and smaller below the flowering nodes, petioles 0.5–2 mm long or the leaves sessile; **leaf blades** 3.5–12 mm long, 1.5–9 mm wide, broadly ovate to broadly oblong, becoming narrower distally (6 × 3 mm), apex rounded to obtuse, margin subentire to obscurely crenate with teeth 0.1–0.2 mm high, obtuse to rounded at the base, glabrous above and below, venation subpalmate. **Inflorescences** 4–15 cm long, erect, racemes or spike-like, rachis appressed puberulent, flowers distant or closely spaced, bracts 2–6 mm long, 1–3 mm wide, narrowly elliptic-oblong to narrowly ovate-elliptic, sessile, glabrous, pedicels 2–4 mm long (–6 mm in fruit), glabrous or puberulent. **Flowers** usually puberulent at the base, calyx lobes 4, subequal, 2–4 mm long, ca. 0.9 mm wide, lanceolate, glabrous or minutely puberulent; **corolla** ca. 4 mm long, lobes 2–4 mm wide, pale blue to blue-purple and with darker lines; styles 1.8–2.5 mm long. **Fruits** 2.3–4 mm long, 3–4.5 mm wide, obovoid with slightly or moderately depressed apex (obcordate), glabrous or minutely puberulent along the distal margins; seeds ovoid, flattened on 1 face, smooth.

Plants of damp open or partly shaded sites in montane forest formations, 2400–3300 m elevation. Probably flowering throughout the year; it is common along the Carretera Interamericana in the Cordillera de Talamanca. This species, a native of western Eurasia, is now widely naturalized in North America and higher elevations in Mexico and Central America.

Veronica serpyllifolia is recognized by its narrow unbranched erect stems, small subentire leaves, short-pedicellate flowers, and subequal oblong calyx lobes. This species is the second most commonly collected species of *Veronica* in Costa Rica.

List of Accepted Species of Scrophulariaceae

Key: END-CR = endemic to continental Costa Rica; END-CR&WP = endemic to Costa Rica and western Panama; END-WP = endemic to western Panama; INTRO = introduced weed; ORNAM = cultivated ornamental; ORNAM & NAT = cultivated and naturalized; ?? = not collected in Costa Rica but known from nearby areas. Total number of species covered is 72; the number of documented native species is 48.

Alectra aspera INTRO
Alonsoa meridionalis
Angelonia angustifolia ORNAM
Anisantherina hispidula
Antirrhinum majus ORNAM

Bacopa axillaris
Bacopa bacopoides ??
Bacopa egensis
Bacopa laxiflora
Bacopa monnieri
Bacopa monnierioides
Bacopa repens
Bacopa salzmännii
Bacopa sessiliflora
Benjaminia reflexa
Buchnera pusilla
Buchnera weberbaueri

Calceolaria irazuensis END-CR
Calceolaria mexicana
Calceolaria microbefaria
Calceolaria perfoliata
Calceolaria tripartita
Capraria biflora
Castilleja arvensis
Castilleja irazuensis END-CR
Castilleja lentii END-CR
Castilleja quirosii END-CR&WP
Castilleja talamancensis END-CR
Castilleja tayloriorum END-CR
Cymbalaria muralis INTRO

Darcya costaricensis END-CR
Darcya reliquiarum END-WP
Digitalis purpurea ORNAM & NAT

Escobedia grandiflora
Hemichaena fruticosa

Lamarouxia gutierrezii END-CR&WP
Lamarouxia lanceolata
Lamarouxia viscosa
Leucocarpus perfoliatus
Limosella acaulis
Linaria canadensis ??
Linaria vulgaris ORNAM
Lindernia crustacea
Lindernia diffusa
Lindernia dubia
Lophospermum erubescens ORNAM & NAT

Maurandya barclaiana ORNAM
Maurandya scandens ORNAM

Mazus pumila INTRO
Mecardonia procumbens
Micranthemum umbrosum ??
Mimulus glabratus ??

Penstemon gentianoides ORNAM

Russelia equisetiformis ORNAM & NAT
Russelia sarmentosa

Schistophragma mexicana
Scoparia annua
Scoparia dulcis
Sibthorpia repens
Stemodia angulata
Stemodia durantifolia
Stemodia peduncularis
Stemodia verticillata

Tetranema floribundum END-CR
Tetranema ganboanum END-CR
Torenia fournieri ORNAM
Torenia thouarsii INTRO

Veronica arvensis INTRO
Veronica peregrina INTRO
Veronica persica INTRO
Veronica polita INTRO
Veronica serpyllifolia INTRO

SCHLEGELIACEAE Reveal

By William Burger and Kerry Barringer

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Shrubs, subshrubs or lianas, erect or climbing, terrestrial or epiphytic, autotrophic, bisexual, stems without internal phloem, glabrous or with simple, eglandular or glandular, unicellular or multicellular hairs, nodes lacking interpetiolar lines or glandular fields; stipules absent. **Leaves** opposite or subopposite, simple, entire (serrulate in *Synapsis*), usually coriaceous to subcoriaceous, glabrous or puberulent, pinnately veined. **Inflorescences** racemes, cymes, or of solitary flowers in leaf axils, sometimes in dense fascicles, bracteoles present, pedicels well developed. **Flowers** bisexual, small to large, often showy, calyx irregularly lobed, 5-lobed or split, persistent and usually accrescent in fruit; **corolla** tubular to funnel-form, bilaterally symmetric or almost radially